
THE TAXONOMIC SIGNIFICANCE OF POLLEN MORPHOLOGY IN THE *COLUMNEA* ALLIANCE (GESNERIACEAE: GESNERIOIDEAE)¹

Karen J. Fritze² and Norris H. Williams^{3,4}

ABSTRACT

Pollen of 67 species of the five genera of the Columnea alliance (Gesneriaceae: Gesnerioideae) was examined to assess its value in generic classifications. Several distinct groups of pollen can be recognized by pollen shape, pattern of exine sculpturing, and shape and size of the colpus. Columnea sensu stricto has a peculiar pollen type supporting its treatment as distinct from the other four genera of the alliance. Bucinellina is also distinct from the other genera, and its status as a genus is likewise supported. Pollen structure does not confirm the distinctiveness of Trichantha, Pentadenia, and Dalbergaria and may be used better at the sectional rather than the generic level.

The mainly tropical family Gesneriaceae contains over 2,800 species. A large influx of collections of newly discovered species from the American tropics has cast doubts on some traditional generic limits in the exclusively neotropical subfamily Gesnerioideae. Parallel adaptations to certain classes of pollinators have become apparent and complicate the efforts of taxonomists. Taking this into consideration, Wiehler (1983) proposed new generic and tribal limits for the Gesnerioideae and a new subfamily (Coronantheroideae). His work parallels Burtt's (1963) for subfamily Cyrtandroideae, and it is in the context of Wiehler's classification that this study was done.

The *Columnea* alliance (tribe Episcieae) is a natural group of closely related genera that share ornithophily as the pollinator syndrome.

The alliance comprises over 240 species in five genera: *Pentadenia* Hanst. (ca. 30 species), *Dalbergaria* Tussac (ca. 90 species), *Trichantha* Hook. (ca. 70 species), *Bucinellina* Wiehler (2 species), and *Columnea* L. (ca. 75 species, Wiehler, 1983). One of the main taxonomic problems in the Episcieae is the disposition of these taxa. Should species distributed variously in several groups formerly regarded as sections of *Columnea* in the broad sense be given generic status, or should they be treated as subgeneric groups of *Columnea*? Morley (1976), who based his conclusions mainly on cytological and hybridization results of Sherk & Lee (1967) and Moore & Lee (1967), disputed treating them as distinct genera. Morton, who worked with *Trichantha* and *Columnea* for a number of years, first lent support to the concept of the

¹ We are grateful to Hans Wiehler for providing plant material and to the Marie Selby Botanical Gardens in Sarasota, Florida, for graciously allowing use of the greenhouses. We thank William Miller for technical assistance with the SEM. Gratitude is due William L. Stern for comments on the manuscript. This publication is based in part on a thesis submitted to Florida State University in partial fulfillment of the requirements for a Master of Science degree by K.J.F. The research was funded in part by NSF grant DEB 7911555 (to N.H.W.) and by a Grant-in-Aid-of-Research from Sigma Xi (to K.J.F.).

² Department of Zoology, University of California, Davis, California 95616, U.S.A.

³ Department of Natural Sciences, Florida State Museum, University of Florida, Gainesville, Florida 32611, U.S.A.

⁴ To whom all correspondence and reprint requests should be sent.

genus *Trichantha* (Morton, 1963) but later reversed his opinion (Morton, 1971). He found that the appendages in the sinuses between corolla lobes that distinguished his concept of *Trichantha* from other taxa were rudimentary throughout the complex. However, Wiehler (1983) maintained that on the basis of several important characters, *Trichantha* and the other four genera are as distinct from one another as from any other genera in the tribe and therefore should be given generic status.

Among the characters Wiehler (1973) considered most important in arriving at generic limits within the *Columnea* alliance and in other Episcieae are fruit type, number of nectary glands present and their degree of dorsal connation, plant habit, and corolla shape. The importance of corolla shape is a source of debate in the classification of the *Columnea* alliance. Within this group, generic limits based on corolla morphology are vague. Although he used it as a convenient means for separating certain genera, Wiehler de-emphasized corolla shape in his overall classification of the subfamily, since it appears to be an adaptation to a pollinator class and is not necessarily indicative of close relationships among taxa. In other words, it is of taxonomic use in separating species but contributes little to an evaluation of systematic relationships. Morley (1973, 1974, 1976), however, believed that degree of corolla zygomorphy is correlated with degree of crossability and is therefore important to classification in the *Columnea* alliance.

Five separate nectary glands distinguish *Pentadenia* from the rest of the Episcieae. All other genera in the Episcieae possess glands which vary in degree of reduction and dorsal connation even within species (Wilson, 1974). In the *Columnea* alliance (except *Pentadenia*) the nectary consists solely of a large double dorsal gland.

The "fern-frond" habit (or extreme anisophylly) makes *Dalbergaria* distinct in the alliance (Wiehler, 1971). Plant habit varies within other genera of the *Columnea* alliance.

Fruit type in the Episcieae is a valuable

suprageneric character. It separates the *Drymonia* complex from the *Episcia* complex, the two having different types of capsules, and separates both from the *Columnea* alliance, which has a berry. Within the *Columnea* alliance genera differ with respect to fruit shape and color. Subtle differences in shape create some skepticism regarding its reliability (Morley, 1976).

Published studies of gesneriaceous pollen are mainly morphological and make little mention of the taxonomic implications. Woods (1964) studied 180 species in over 50 genera and made a distinction between Burt's subfamilies based on pollen-wall sculpturing and grain size. Uniform or homobrochate exines are more prevalent in the Cyrtandroideae; heterobrochate exines are more prevalent in the Gesnerioideae. Grains tend to be larger in the Gesnerioideae than in the Cyrtandroideae.

Erdtman (1966) surveyed 20 species from 17 genera of the Gesneriaceae with the light microscope and supplied a diagram of *Columnea microphylla* pollen. Melhem & Mauro (1973) obtained data on eight local species from three genera in São Paulo, Brazil. Based on their observations and those of Erdtman, they concluded that there was great variation of pollen types in the family. They remarked only on morphological distinctions among pollen of these species and included no taxonomic interpretations.

Skog (1976), in his taxonomic treatment of the tribe Gesnerieae, presented a brief discussion of his observations on the grains of 27 examples. He made use of the scanning electron microscope, but little information could be obtained from his micrographs other than sculpturing patterns, since the pollen grains were collapsed.

The absence of pollen data from Wiehler's (1973) study prompted a preliminary SEM survey by Williams (1978) of 30 species representing 19 genera to ascertain whether or not pollen might be of use in further clarifying systematic relationships in the Gesnerioideae. Williams (1978) found a wide variety of forms in the Gesneriaceae, particularly in tribe Epi-

TABLE 1. *Species examined.*

Species	Greenhouse Accession Number	Origin
<i>Columnnea arguta</i> C. Morton	G-979 SEL	Panama
<i>C. bilabiata</i> Seemann	W-2233 SEL	Colombia
<i>C. billbergiana</i> Beurling	W-1166 SEL	Panama
<i>C. cobana</i> F. D. Smith	W-2056 SEL	Guatemala
<i>C. dodsonii</i> Wiehler	W-1500 SEL	Ecuador
<i>C. dressleri</i> Wiehler	W-2176 SEL	Panama
<i>C. erythrophaea</i> Decne.	G-1057 SEL	Mexico
<i>C. flaccida</i> Seemann	G-327 SEL	Panama
<i>C. gallicauda</i> Wiehler	W-2179 SEL	Panama
<i>C. gloriosa</i> Sprague	W-2131 SEL	Panama
<i>C. guatemalensis</i> Sprague	W-2055 SEL	Guatemala
<i>C. hirsutissima</i> C. Morton	W-2132 SEL	Panama
<i>C. kienastiana</i> Regel	W-1694 SEL	Colombia
<i>C. kucyniakii</i> Raym.	W-2020 SEL	Ecuador
<i>C. linearis</i> Oersted	G-325 SEL	Costa Rica
<i>C. maculata</i> C. Morton	W-2262 SEL	Panama
<i>C. nicaraguensis</i> Oersted	W-2641 SEL	Panama
<i>C. oerstediana</i> Klotzsch ex Oersted	W-2270 SEL	Panama
<i>C. purpusii</i> Standley	G-1209 SEL	Mexico
<i>C. querceti</i> Oersted	W-2641 SEL	Costa Rica
<i>C. repens</i> (Hook.) Hanst.	G-920 SEL	Jamaica
<i>C. rubra</i> C. Morton	W-2236 SEL	Panama
<i>C. rubricaulis</i> Standley	W-2328 SEL	Nicaragua
<i>C. rutilans</i> Sw.	G-843 SEL	Jamaica
<i>C. schiedeana</i> Schldl.	G-725 SEL	Mexico
<i>C. verecunda</i> C. Morton	G-87 SEL	Costa Rica
<i>C. zebranella</i> Wiehler	W-1595 SEL	Panama
<i>Dalbergaria asteroloma</i> Wiehler	W-2247 SEL	Ecuador
<i>D. aureonitens</i> (Hook.) Wiehler	W-1818 SEL	Venezuela
<i>D. cruenta</i> (Morley) Wiehler	W-1146 SEL	Panama
<i>D. eburnea</i> Wiehler	W-1704 SEL	Colombia
<i>D. ericae</i> (Mansf.) Wiehler	W-1630 SEL	Ecuador
<i>D. florida</i> (C. Morton) Wiehler	W-1622 SEL	Panama
<i>D. inaequilatera</i> (Poeppig) Wiehler	W-2036 SEL	Ecuador
<i>D. kahlbreyeriana</i> (Masters) Wiehler	W-1590 SEL	Colombia
<i>D. perpulchra</i> (C. Morton) Wiehler	W-1572 SEL	Panama
<i>D. picta</i> (Karsten) Wiehler	W-1794 SEL	Colombia
<i>D. polyantha</i> Wiehler	W-1152 SEL	Panama
<i>D. puyana</i> Wiehler	W-2040 SEL	Ecuador
<i>D. sanguinea</i> (Pers.) Steudel	W-1709 SEL	Panama
<i>D. sanguinea</i> (Pers.) Steudel	G-85 SEL	Hispaniola
<i>D. sanguinea</i> (Pers.) Steudel	W-1628 SEL	Panama
<i>D. silvarum</i> (C. Morton) Wiehler	W-2450 SEL	Panama
<i>D. vittata</i> Wiehler	W-2265 SEL	Panama
<i>Pentadena augustata</i> Wiehler	W-2185 SEL	Costa Rica
<i>P. byrsina</i> Wiehler	W-2138 SEL	Ecuador
<i>P. ecuadorana</i> Wiehler	W-1894 SEL	Ecuador
<i>P. microsepala</i> (C. Morton) Wiehler	W-1837 SEL	Venezuela
<i>P. nervosa</i> Kl. ex Oersted	W-1948 SEL	Panama
<i>P. orientandina</i> Wiehler	W-2273 SEL	Ecuador
<i>P. spathulata</i> (Mansf.) Wiehler	W-1955 SEL	Ecuador
<i>P. strigosa</i> (Benth.) Hanst.	W-4128 SEL	Colombia
<i>P. zapotaliana</i> Wiehler	W-2167 SEL	Ecuador
<i>Trichantha ambigua</i> (Urban) Wiehler	G-804 SEL	Puerto Rico

TABLE 1. *Continued.*

Species	Greenhouse Accession Number	Origin
<i>T. brenneri</i> Wiehler	W-2275 SEL	Ecuador
<i>T. calotrica</i> (F. D. Smith) Wiehler	W-2181 SEL	Panama
<i>T. citrina</i> Wiehler	W-2451 SEL	Panama
<i>T. dissimilis</i> (C. Morton) Wiehler	W-1177 SEL	Panama
<i>T. filifera</i> Wiehler	W-1631 SEL	Colombia
<i>T. herthae</i> (Mansf.) Wiehler	W-1573 SEL	Ecuador
<i>T. minor</i> Hook.	W-1685 SEL	Colombia
<i>T. mira</i> (Morley) Wiehler	W-1586 SEL	Panama
<i>T. moorei</i> (C. Morton) C. Morton	W-2193 SEL	Panama
<i>T. parviflora</i> (C. Morton) Wiehler	W-1993 SEL	Panama
<i>T. pulchra</i> Wiehler	W-2368 SEL	Panama
<i>T. purpureovittata</i> Wiehler	W-1721 SEL	Peru
<i>T. tenensis</i> Wiehler	W-1585 SEL	Ecuador
<i>Bucinellina nariniana</i> (Wiehler) Wiehler	W-1642 SEL	Colombia
<i>B. paramicola</i> (Wiehler) Wiehler	W-1634 SEL	Colombia

scieae. Fritze (1979) found the diversity of pollen to be of potential taxonomic use in the *Columnea* alliance, and Williams (1978) introduced a successful technique for preparing gesneriaceous pollen that shows expanded, clean grains and allows full observation of all external features.

MATERIALS AND METHODS

Pollen was collected from mature anthers of living plants grown in the greenhouses at the Marie Selby Botanical Gardens, Sarasota, Florida (Table 1). The pollen was acetolyzed following a modified method of Erdtman (1966) and was stored in 70% ethyl alcohol (EtOH). Slides for vouchers were made from which sizes and shapes of pollen grains could be determined. Measurements of the lengths of the polar and equatorial axes of 50 grains per species of representative species were made at 400× using an ocular micrometer. Pollen for the scanning electron microscope (SEM) was dehydrated through an alcohol series followed by an amyl acetate/EtOH series (1:3, 1:1, 3:1, 100% amyl acetate). A drop of suspended pollen was then placed on a round glass coverslip and attached to an SEM stub with double-sided tape. The pollen was air dried under a cover to prevent contamination. Dried pollen was coated with 5

nm of gold palladium and scanned with a Cambridge Stereoscan model S4-10 instrument at 5, 10, or 20 kV. Fractured pollen was also viewed with the SEM. Pollen was transferred from the original SEM stub to a second stub fitted with a piece of double-sided tape covering the entire surface. Transfer was accomplished by touching the two stubs together until the pollen adhered to the tape. The process was repeated using a third stub with double-sided tape on it, which was pressed against the second stub. The adhesion of the pollen grains to both stubs pulled the grains apart. This procedure requires no elaborate microtomy and yields replicates with no loss of material. The fractured grains were re-coated and scanned. Photographs were taken using Type 665 Positive/Negative Land film with a Polaroid camera mounted on the microscope, and negatives were later contact printed.

NOTE ON TERMINOLOGY

Terminology used for the apertures, shape, and areas of the surface of the pollen grain follows Erdtman (1966). Since Erdtman's terms do not extend to the detail of exine sculpturing revealed by the SEM, it is necessary to make a precise distinction between the punctate and reticulate patterns found in

the *Columnea* alliance. An exine is punctate if the tectum is perforate and the majority of the perforations are much smaller in diameter than the width of the muri (remnants of the tectum). The exine is reticulate if the punctae are enlarged (lumina) and at least as wide as the muri. A long aperture extends beyond half the distance from the equatorial margin of the grain to the polar axis when seen in polar view (Fig. 2E). An aperture of intermediate length reaches about one-half this distance (Fig. 8C), and a short aperture extends less than half this distance (Fig. 12G, H). Terms describing exine structure follow Walker (1974a)

RESULTS AND OBSERVATIONS

Several pollen types appeared with some overlap among genera. Types are distinguished mainly by shape, exine pattern, and aperture length and shape. All grains are monads, isopolar, and tricolp(or)ate, and either punctate or reticulate. Their sizes, based on the length of the longest axis, range from approximately 28 to 51 μm . The features are summarized for each species in Table 2.

By far the greatest homogeneity turned up

in *Columnea*, in which 26 species were examined (Figs. 1, 2, 3, 4, 5A–C). With the exception of three species, all have subprolate to spheroidal grains (see P/E, Table 2) with uniformly punctate exine, long, elliptic apertures, and circular amb. There are slight differences in size and shape of punctae and apertures between species. *Columnea repens* and *C. rutilans* (Fig. 5B, C) stand apart by having suboblate or oblate grains, exine reticulate grading to punctate adjacent to the colpi and at the polar regions, tapered apertures, and triangular amb. *Columnea kucyniakii* has suboblate grains, exine reticulate grading to punctate adjacent to the colpi and poles, long, sharply tapered apertures, and triangular amb.

The majority of the 15 *Dalbergaria* species examined (Figs. 5D–H, 6, 7, 8) have grains distinct from those of *Columnea*. Those of the former are suboblate and have the exine reticulate grading to punctate adjacent to the colpi and at the poles, long, sharply tapered apertures, and angularaperturate, circular or triangular amb. *Dalbergaria aureonitens*, *D. sanguinea*, and *D. florida* (Fig. 8) do not fit the general pattern; they have pollen suboblate to spheroidal, reticulate (as above, but

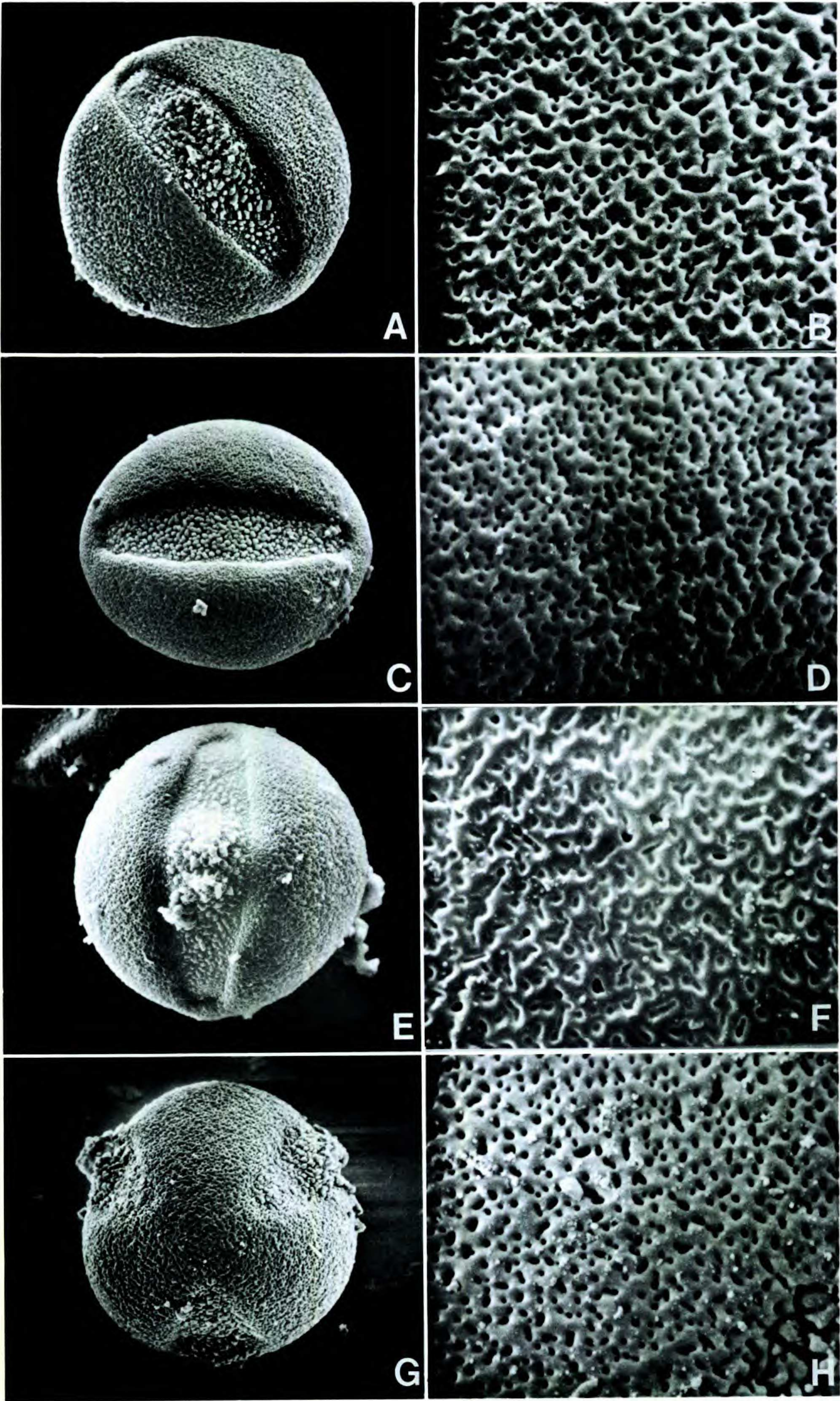
FIGURE 1.—A. *Columnea schiedeana*, equatorial view; $\times 1,550$.—B. *C. schiedeana*, mesocolpial region; $\times 7,333$.—C. *C. verecunda*, equatorial view; $\times 1,550$.—D. *C. verecunda*, mesocolpial region; $\times 7,333$.—E. *C. querceti*, equatorial view; $\times 1,387$.—F. *C. querceti*, mesocolpial region; $\times 7,333$.—G. *C. purpusii*, polar view; $\times 1,500$.—H. *C. purpusii*, mesocolpial region; $\times 7,333$.

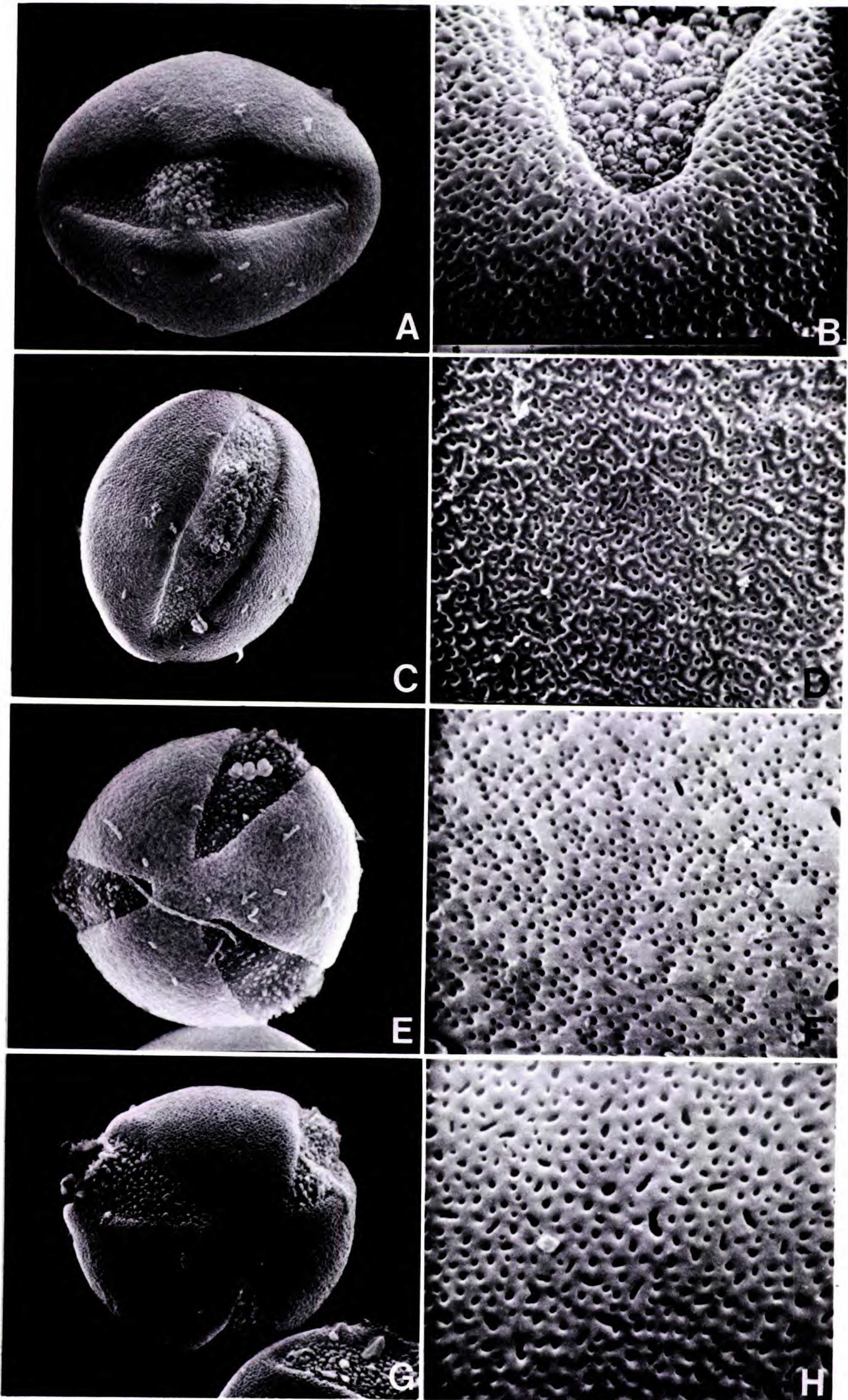
FIGURE 2.—A. *Columnea arguta*, equatorial view; $\times 1,300$.—B. *C. arguta*, at end of colpus; $\times 5,717$.—C. *C. guatemalensis*, equatorial view; $\times 1,333$.—D. *C. guatemalensis*, mesocolpial region; $\times 6,833$.—E. *C. cobana*, polar view; $\times 1,383$.—F. *C. cobana*, mesocolpial region; $\times 7,000$.—G. *C. kienastiana*, polar view; $\times 1,500$.—H. *C. kienastiana*, mesocolpial region; $\times 8,000$.

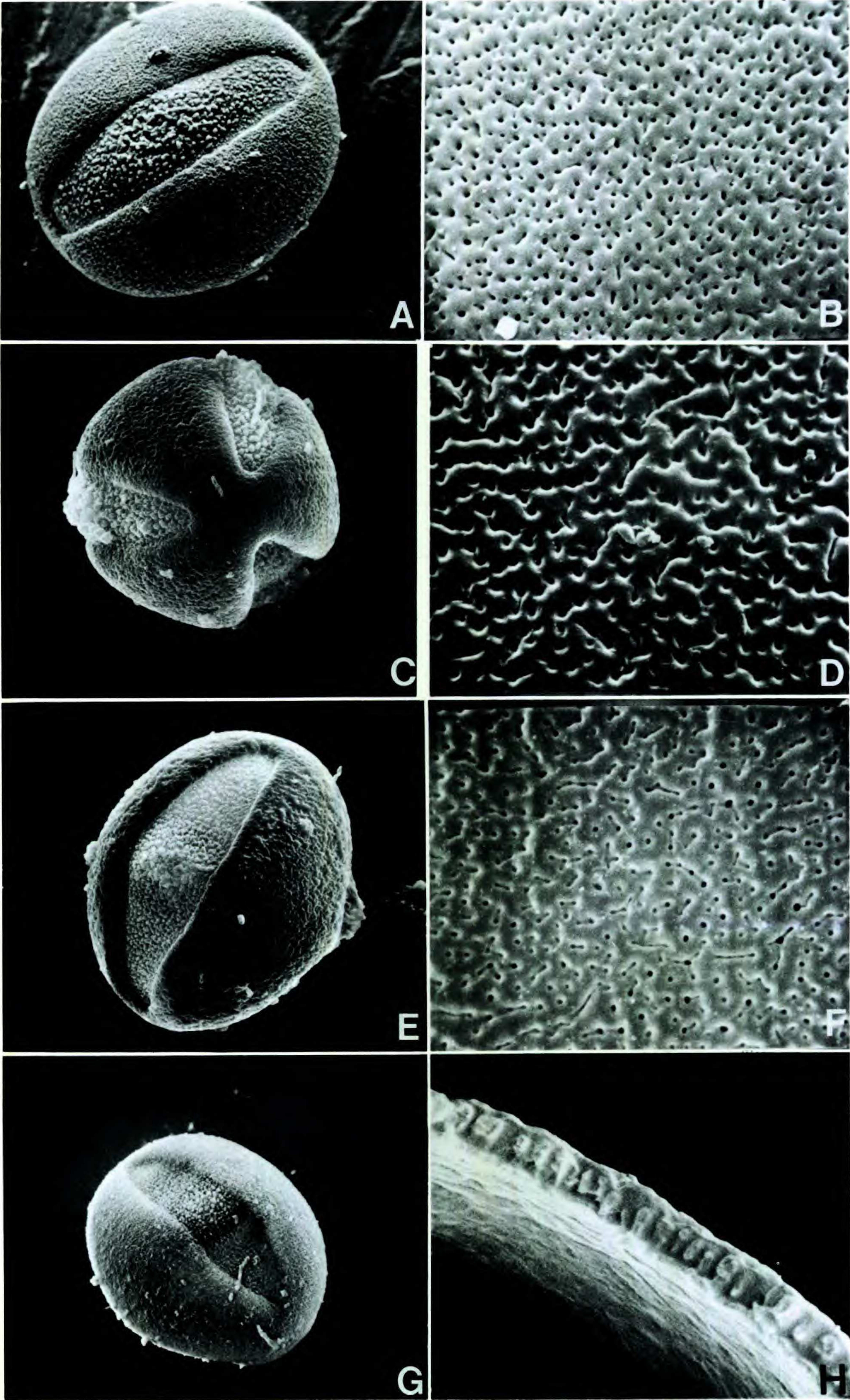
FIGURE 3.—A. *Columnea linearis*, equatorial view; $\times 1,567$.—B. *C. linearis*, mesocolpial region; $\times 7,333$.—C. *C. hirsutissima*, polar view; $\times 1,433$.—D. *C. hirsutissima*, mesocolpial region; $\times 6,867$.—E. *C. dressleri*, equatorial region; $\times 1,333$.—F. *C. dressleri*, mesocolpial region; $\times 6,667$.—G. *C. dodsonii*, equatorial view; $\times 7,833$.—H. *C. dressleri*, exine fracture through mesocolpial region; $\times 10,000$.

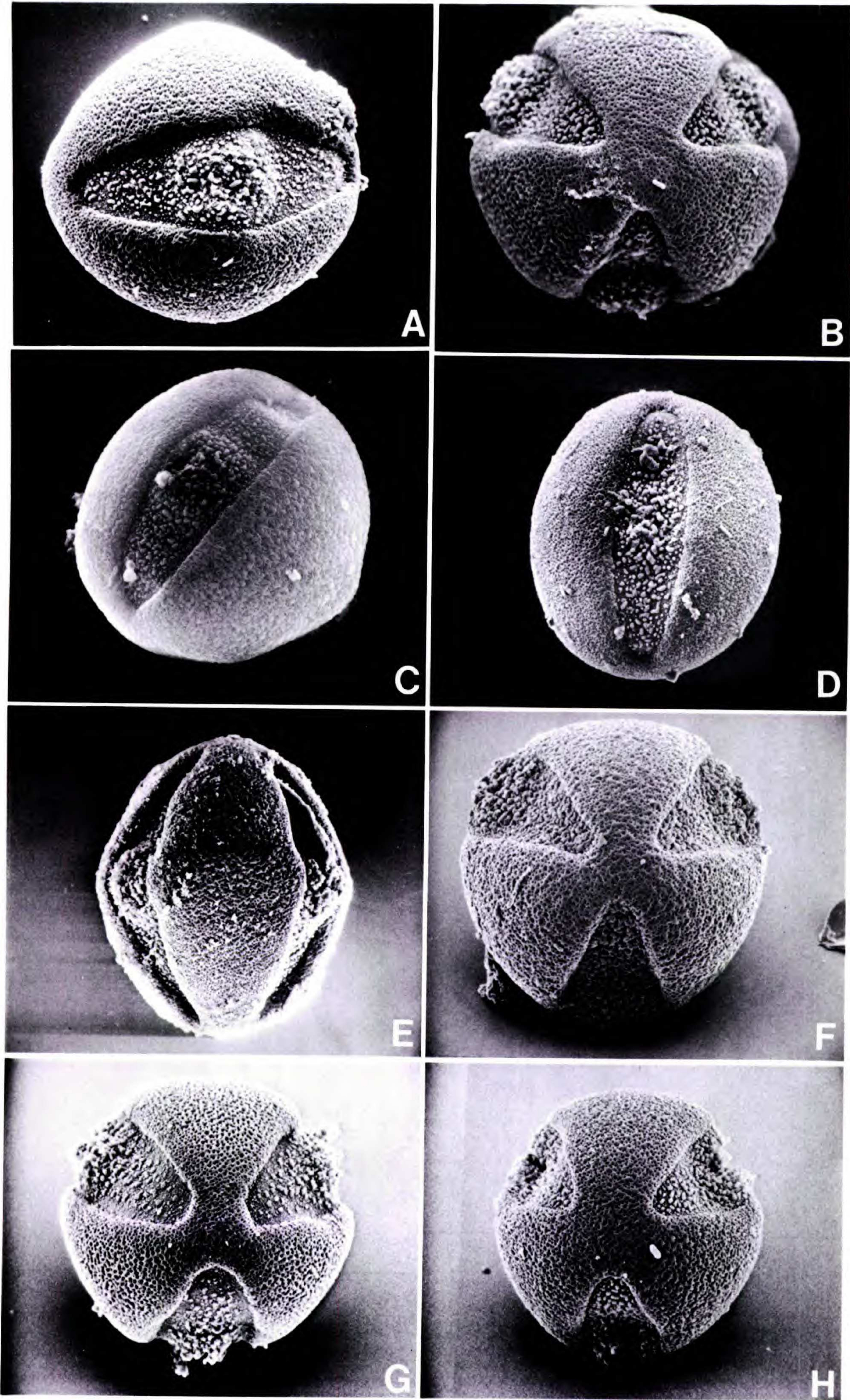
FIGURE 4.—A. *Columnea gallicauda*, equatorial view; $\times 1,383$.—B. *C. zebranella*, polar view; $\times 1,687$.—C. *C. flaccida*, equatorial view; $\times 1,483$.—D. *C. rubricaulis*, equatorial view; $\times 1,383$.—E. *C. oerstediana*, equatorial view; $\times 1,307$.—F. *C. bilabiata*, polar view; $\times 1,467$.—G. *C. rubra*, polar view; $\times 1,433$.—H. *C. erythrophaea*, polar view; $\times 1,500$.

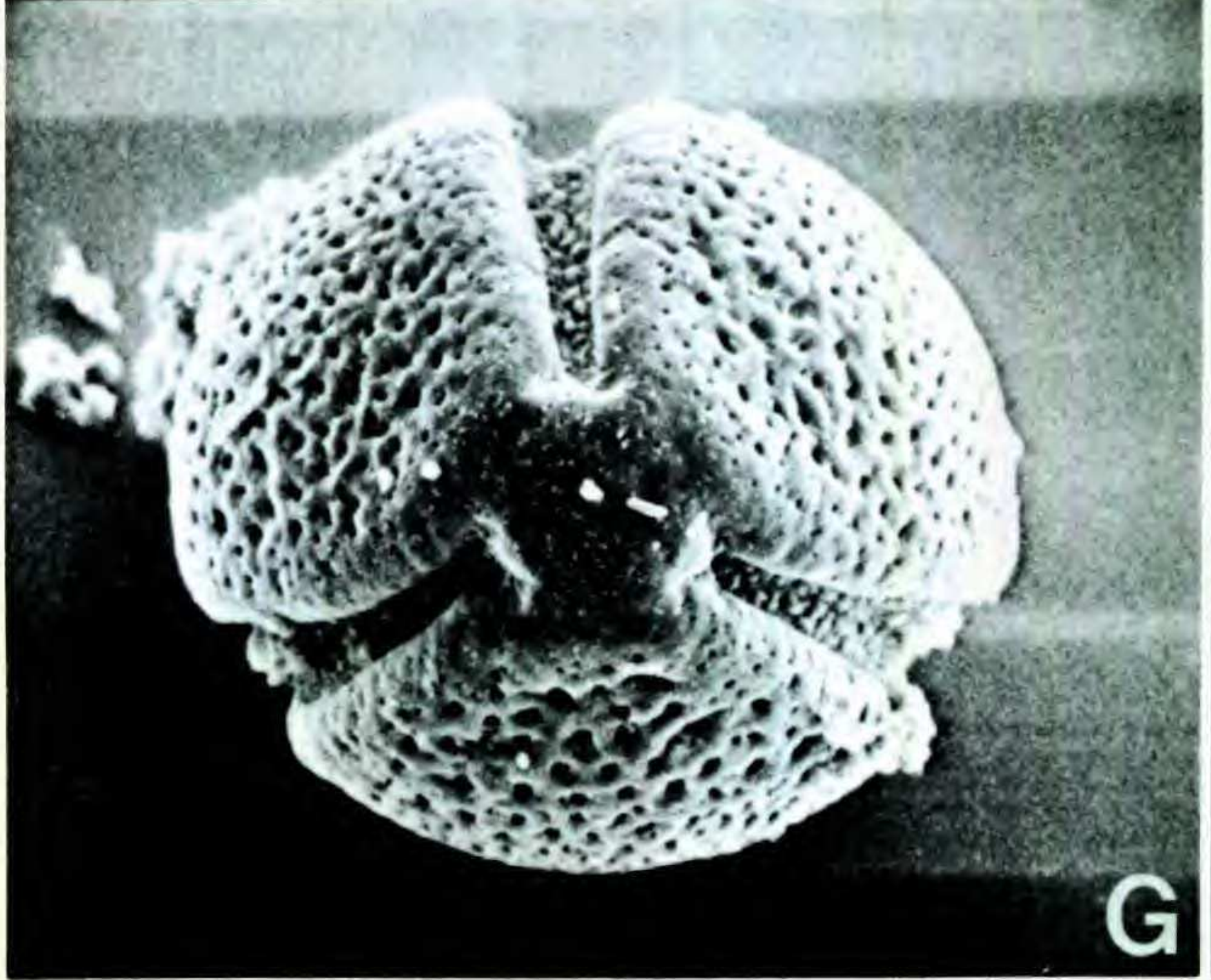
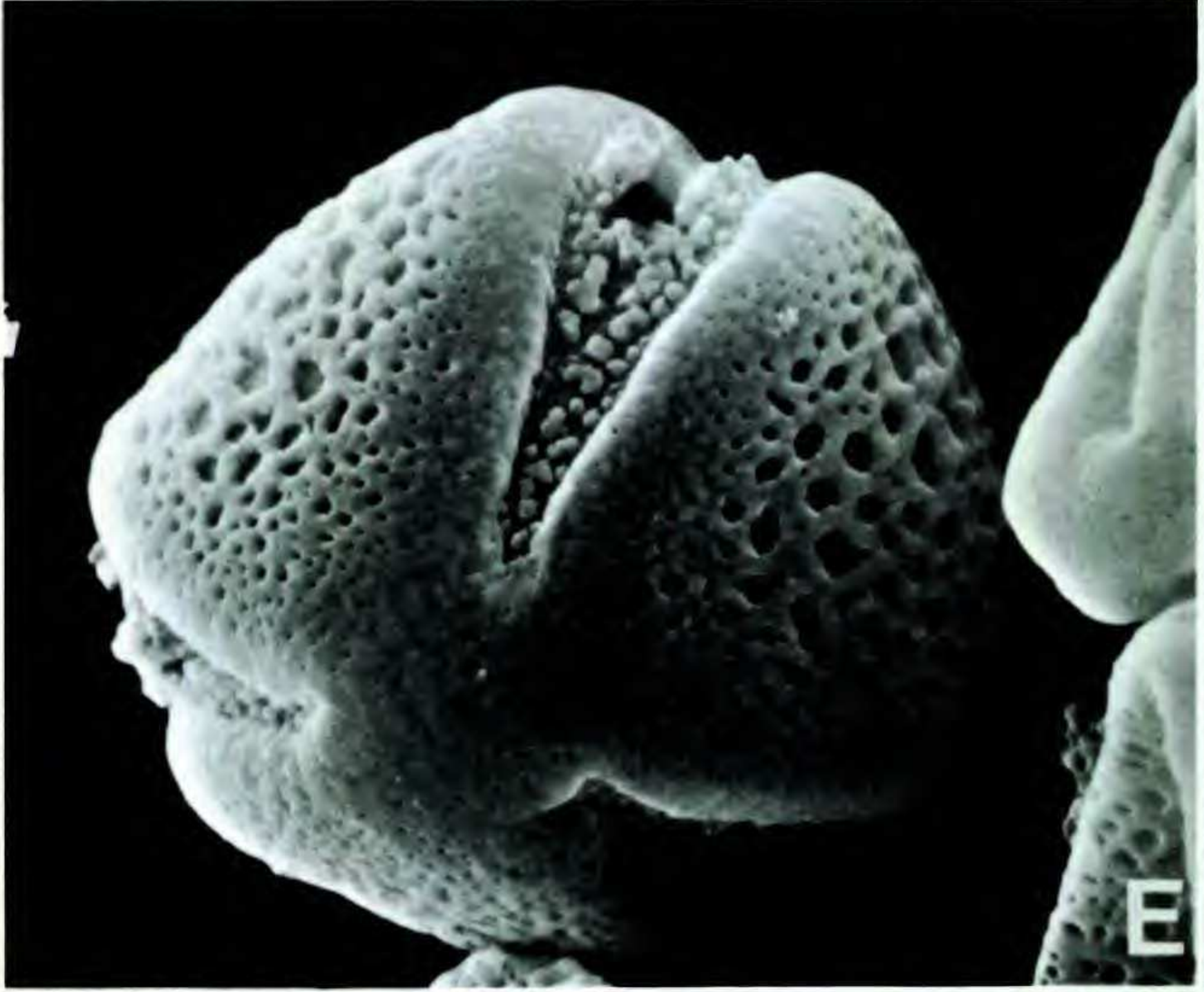
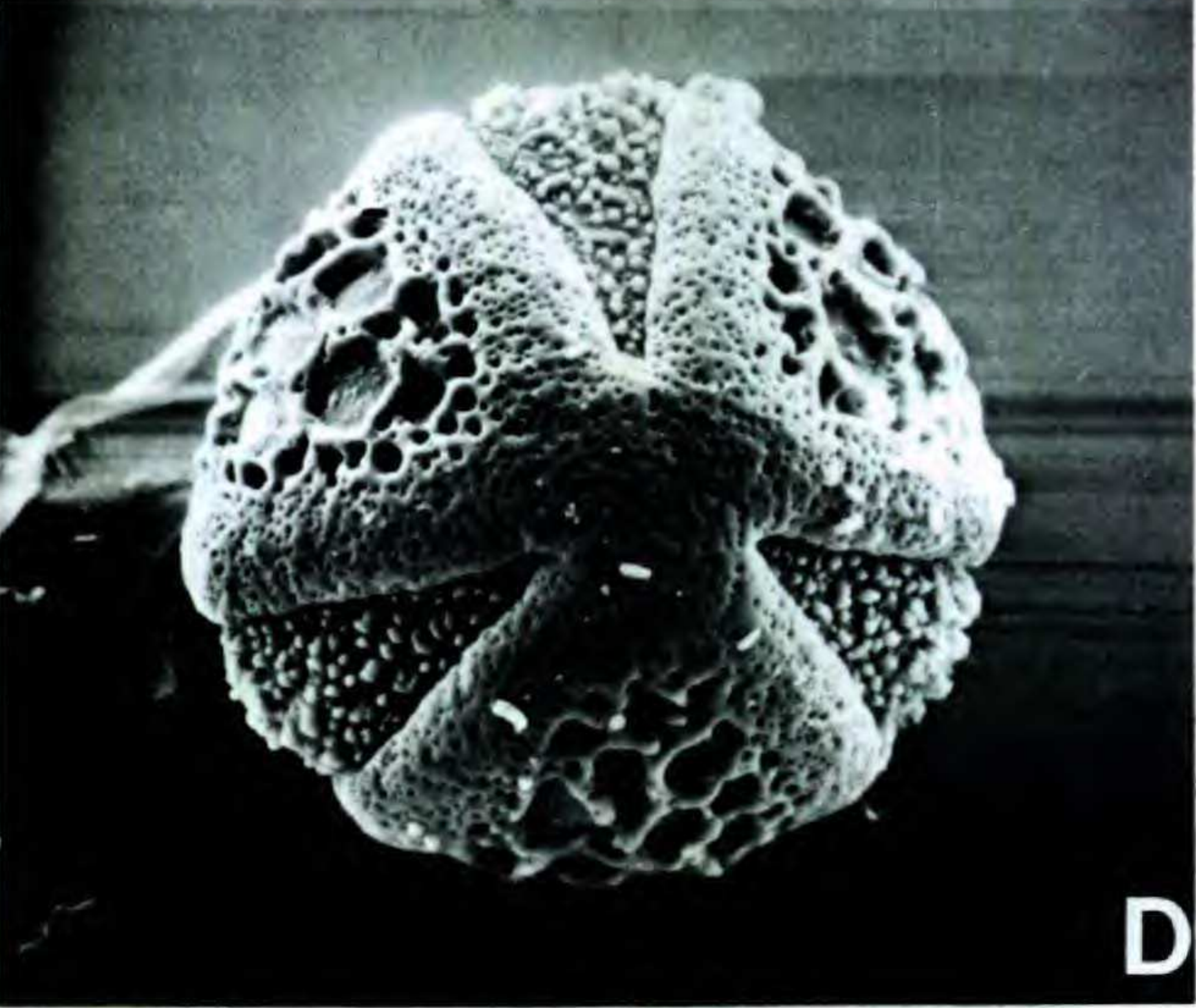
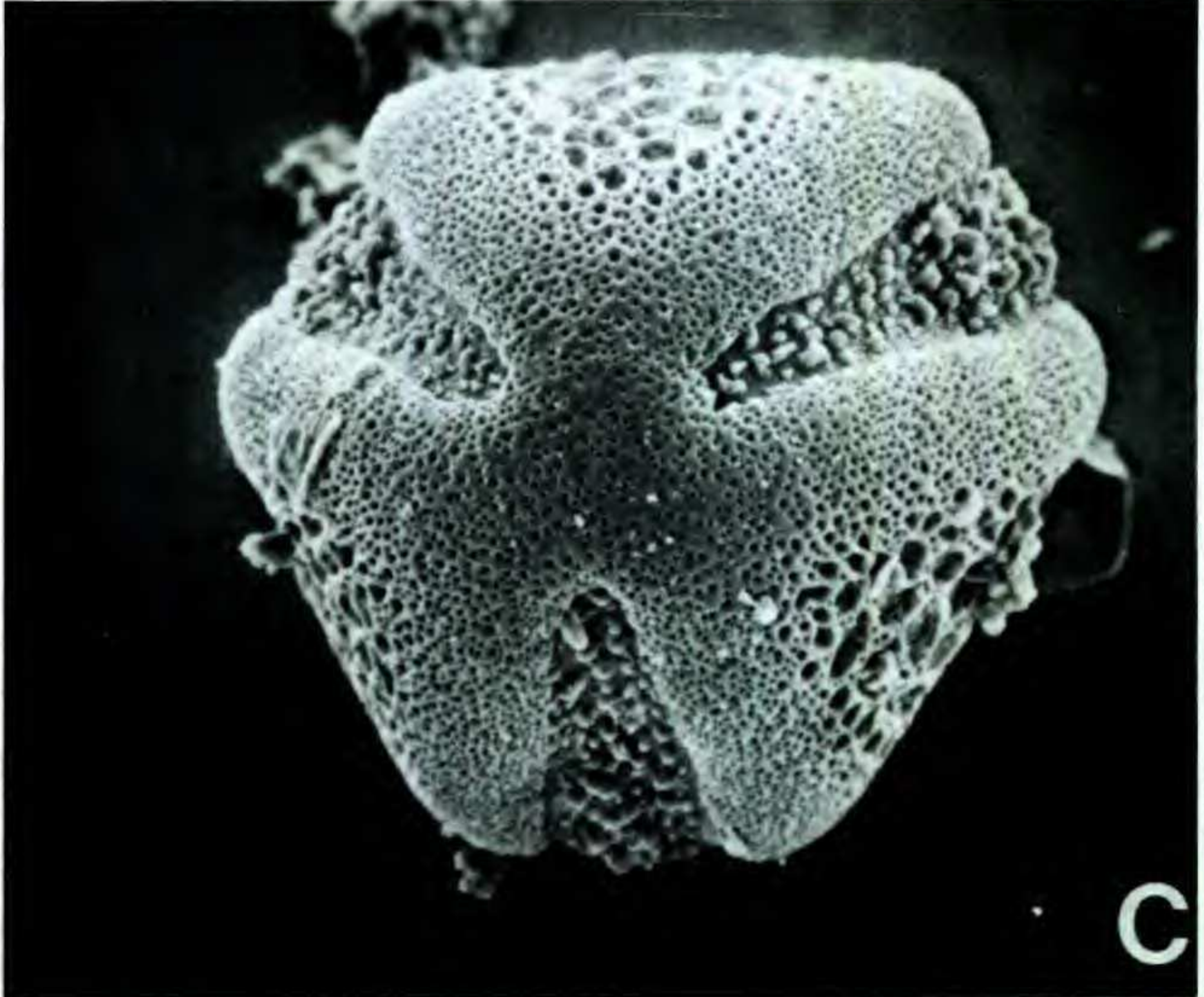
FIGURE 5.—A. *Columnea billbergiana*, equatorial view; $\times 1,316$.—B. *C. repens*, polar view; $\times 1,233$.—C. *C. rutilans*, polar view; $\times 1,300$.—D. *Dalbergaria silvarum*, polar view; $\times 1,493$.—E. *D. puyana*, polar view; $\times 1,733$.—F. *D. polyantha*, polar view; $\times 1,450$.—G. *D. asteroloma*, polar view; $\times 1,350$.—H. *D. ericae*, exine fracture through colpus; $\times 8,000$.











the reticulation not reduced to punctae at the poles), and with the colpi more elliptic, these of intermediate length. *Dalbergaria eburnea* (Fig. 7E, F) and *D. asteroloma* (Fig. 5G) grains are suboblate to spheroidal with the tectum nearly punctate, tectal perforations near the colpi and at the poles reduced in size or absent, and the apertures narrow.

Three distinct types of pollen are found within *Trichantha* (15 species examined). One type (Figs. 9A–G, 10E) is suboblate with a reticulate exine becoming punctate adjacent to the colpi and at the poles and has long apertures widest at the equator and a triangular amb. These grains resemble pollen of *Dalbergaria* and *Pentadenia orientandina*. *Trichantha ambigua*, a tetraploid, has pollen of this type but with four apertures (Fig. 10C). A second type of pollen with short colpi (Fig. 10A, B, G, H) is oblate to spheroidal, reticulate, and punctate around the colpi with intermediate elliptic apertures; this type has a somewhat triangular amb. The third type (Fig. 11A–D) is suboblate and punctate, and has very short oval apertures (almost like pores); its amb is circular to slightly triangular.

Most species of *Pentadenia* (9 species ex-

amined) possess suboblate to oblate grains that are reticulate, becoming punctate adjacent to the colpi but remain reticulate at the poles; they have either short or intermediate apertures and somewhat triangular amb (Figs. 12A–H, 13C, D). *Pentadenia ecuadorana* (Fig. 12C, D), *P. microsepala* (Fig. 12E, F), and *P. angustata* (Fig. 13C) grains have narrow apertures of intermediate length, but the apertures are widest at the equator. Grains of *Pentadenia spathulata* (Fig. 12G) and *P. zapotalana* (Fig. 12H) have short elliptic apertures. *Pentadenia orientandina* pollen (Fig. 13A, B) is suboblate and reticulate, grading to punctate at the poles and adjacent to the colpi; it has long luminal baculae, long apertures tapered at the poles, and circular amb. It stands apart from other pentadenias and resembles some *Trichantha* pollen types (e.g., Fig. 9). *Pentadenia strigosa* (Fig. 13E, F) pollen shows a combination of features found nowhere else in the *Columnnea* alliance. The pollen is suboblate and reticulate with long luminal baculae, and the reticulum is neither reduced at the poles nor around the colpi. It has long, elliptic, slightly tapered apertures and a circular amb.

Bucinellina, with only two species (Fig.

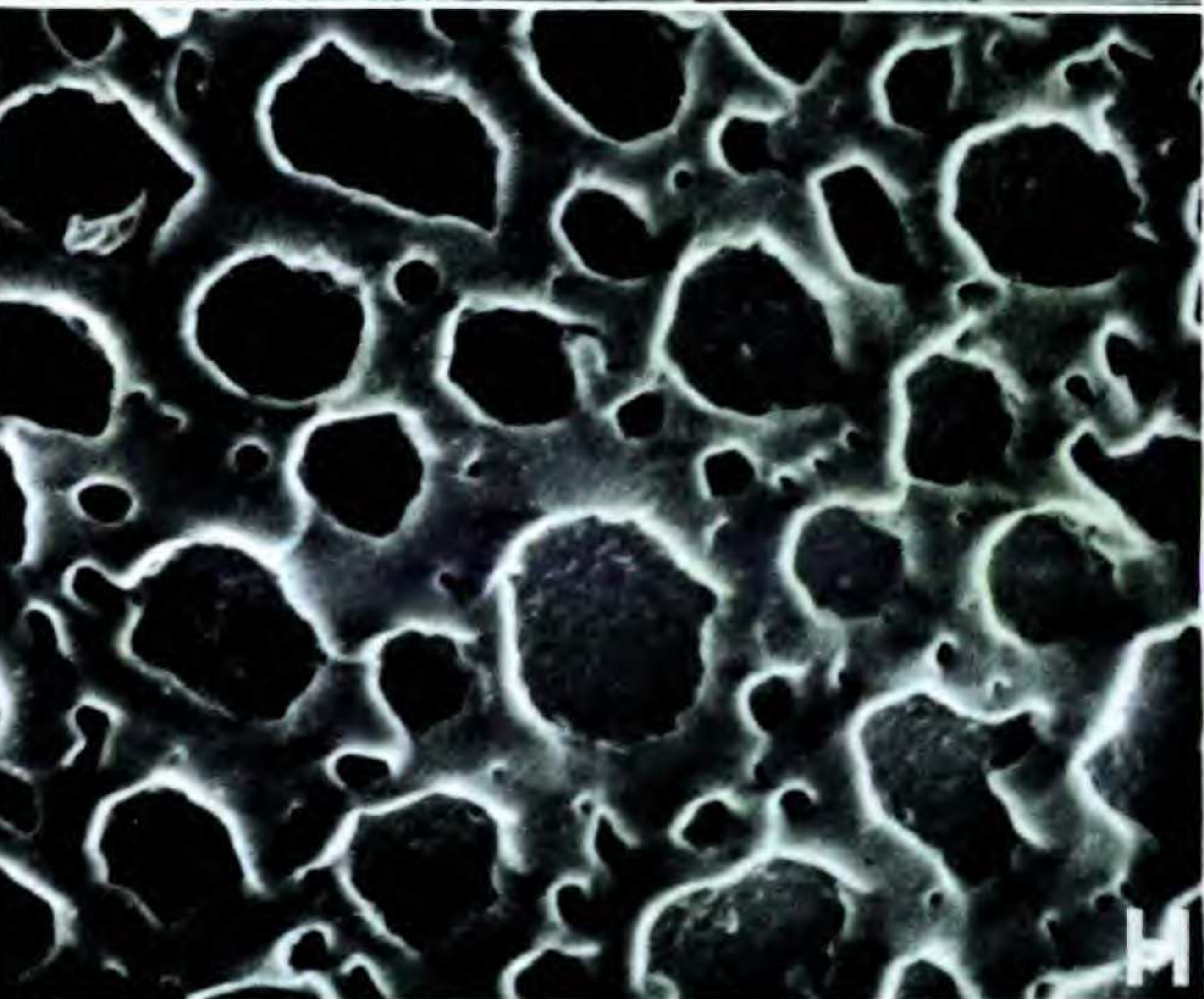
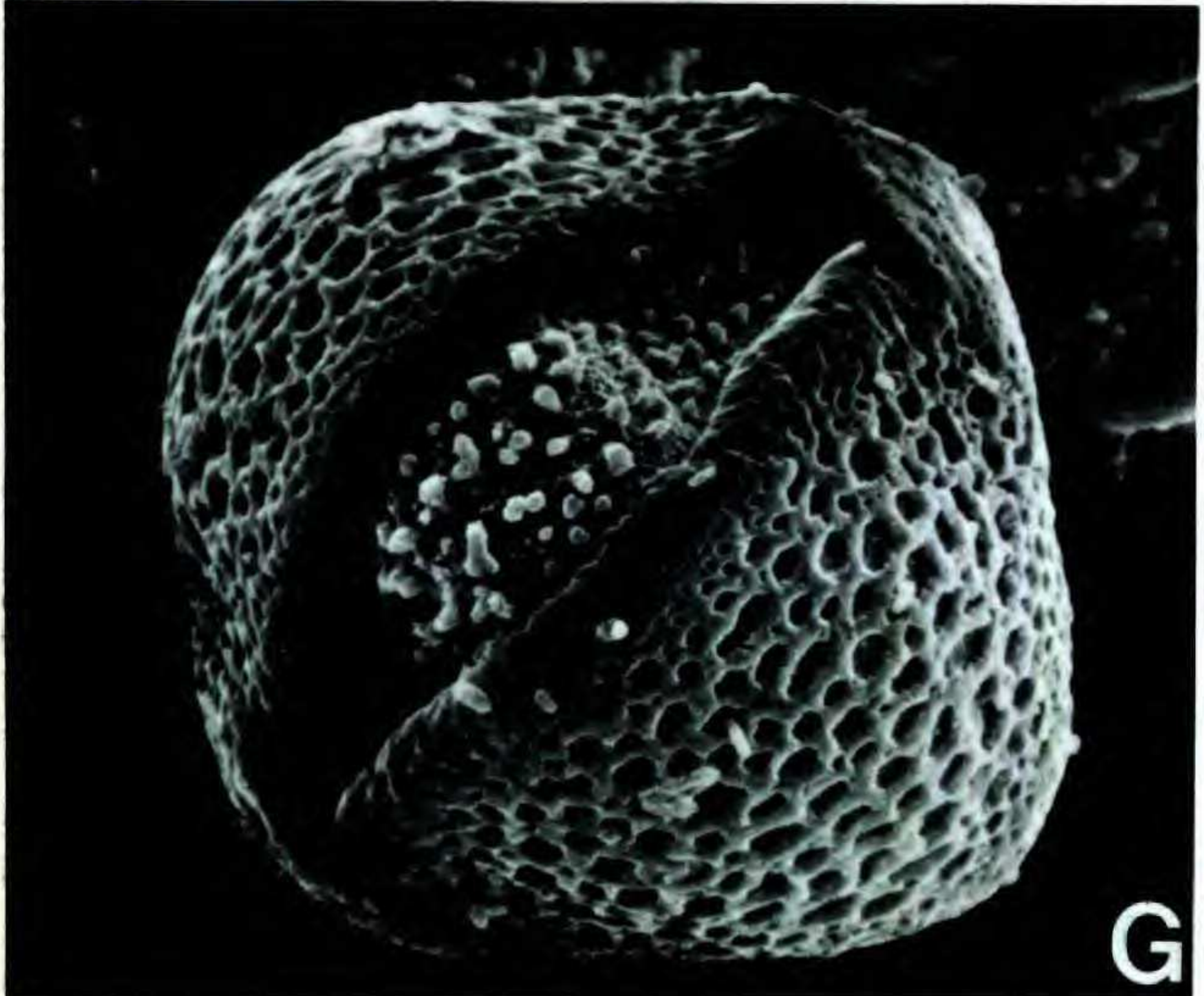
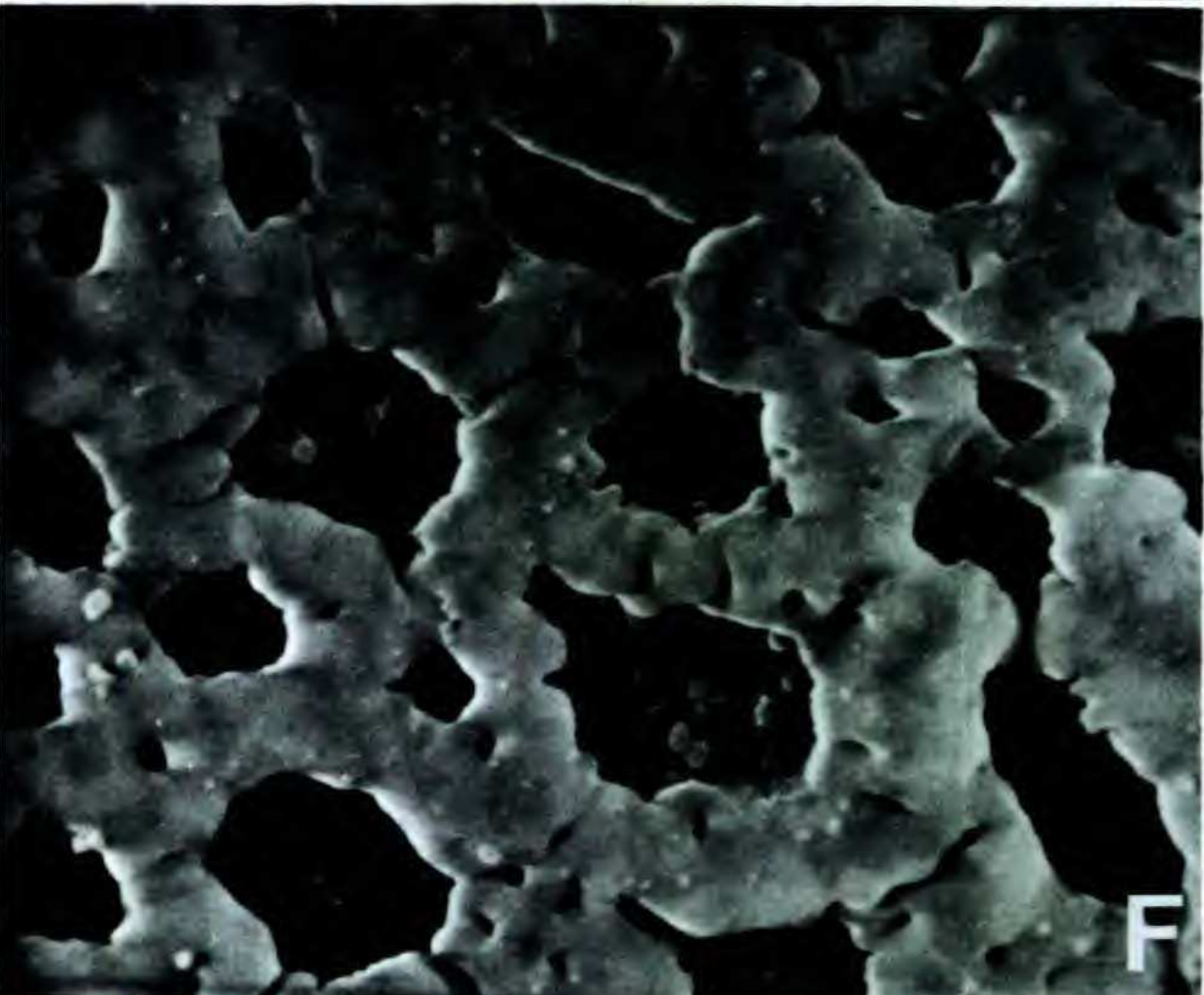
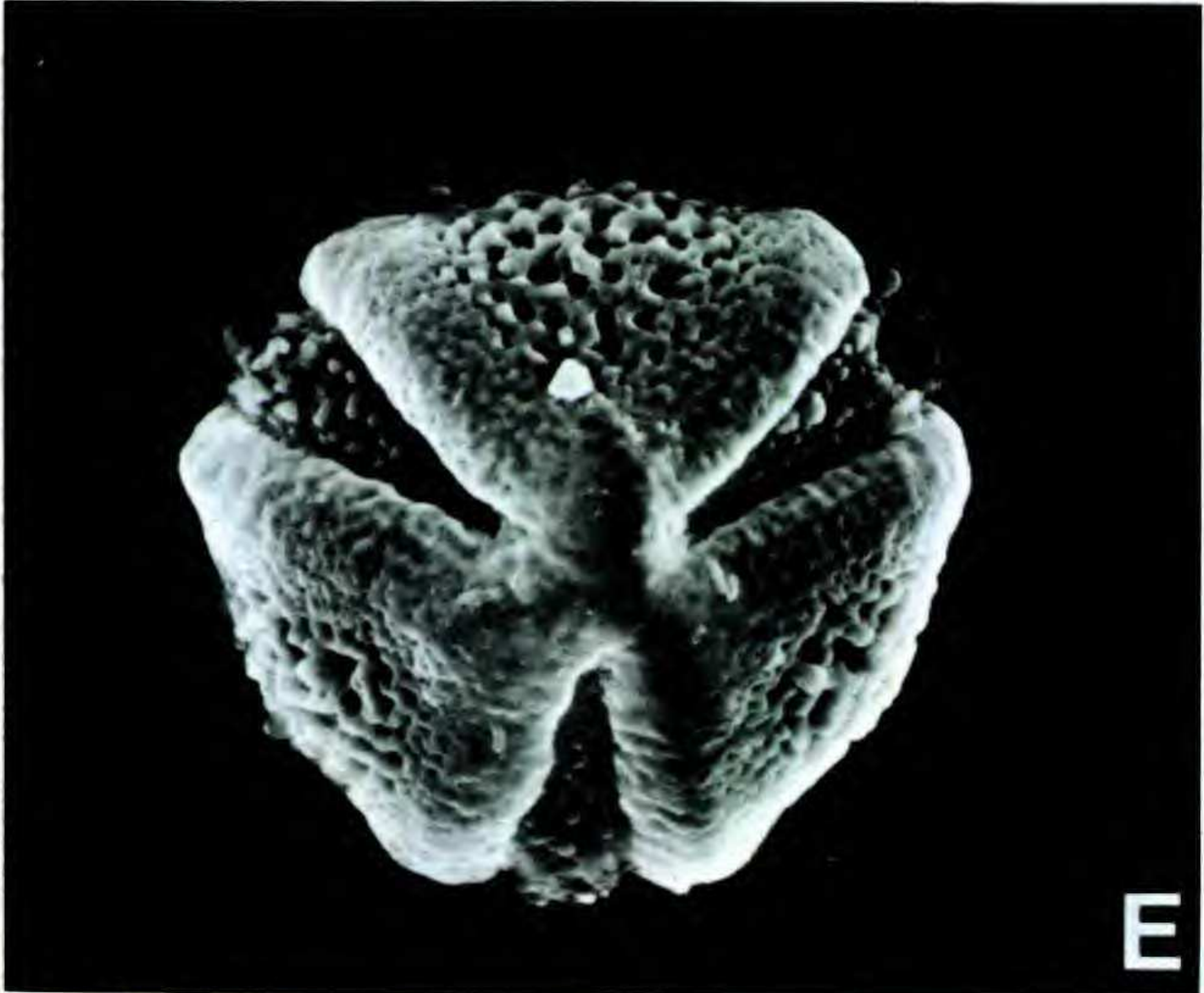
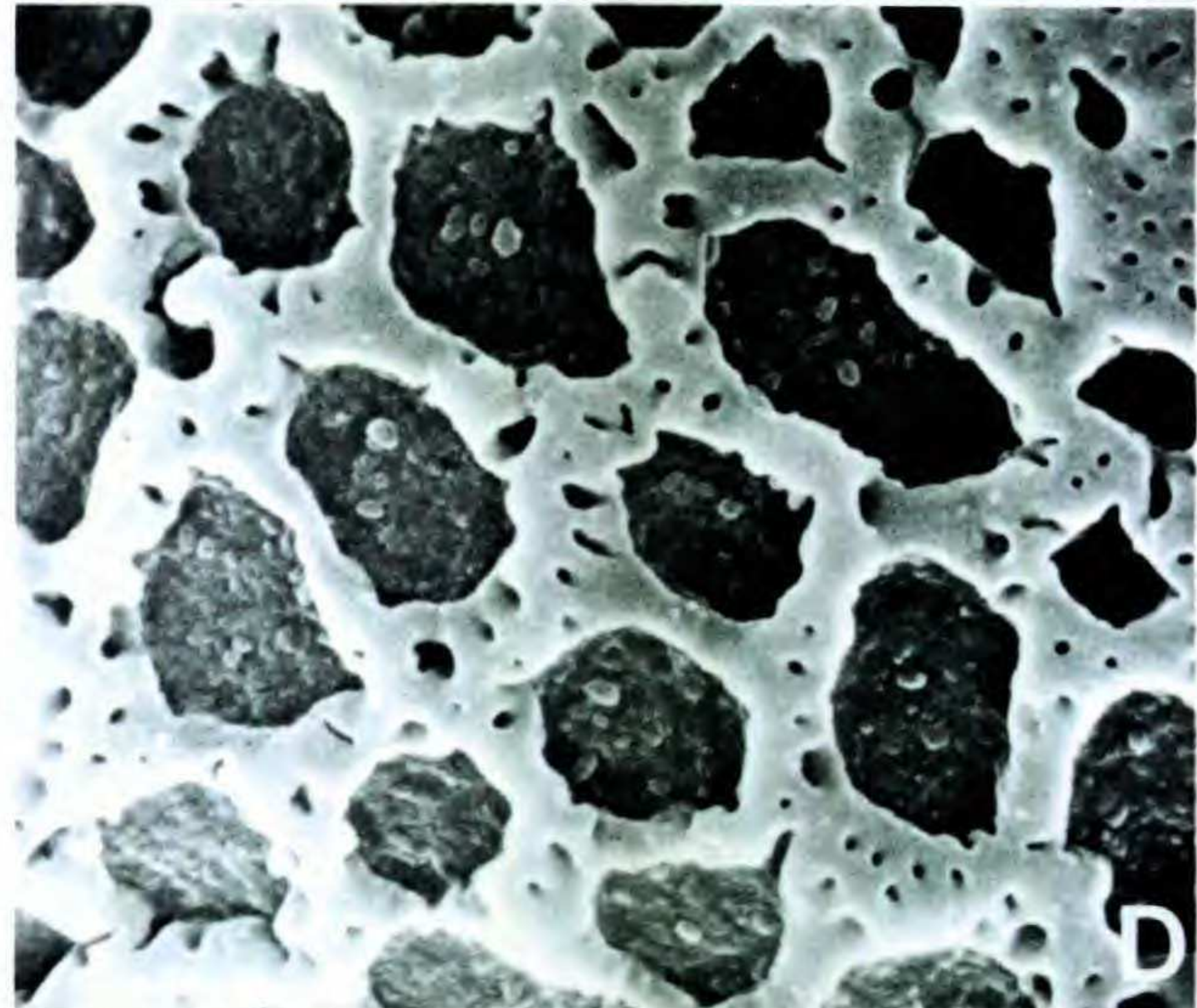
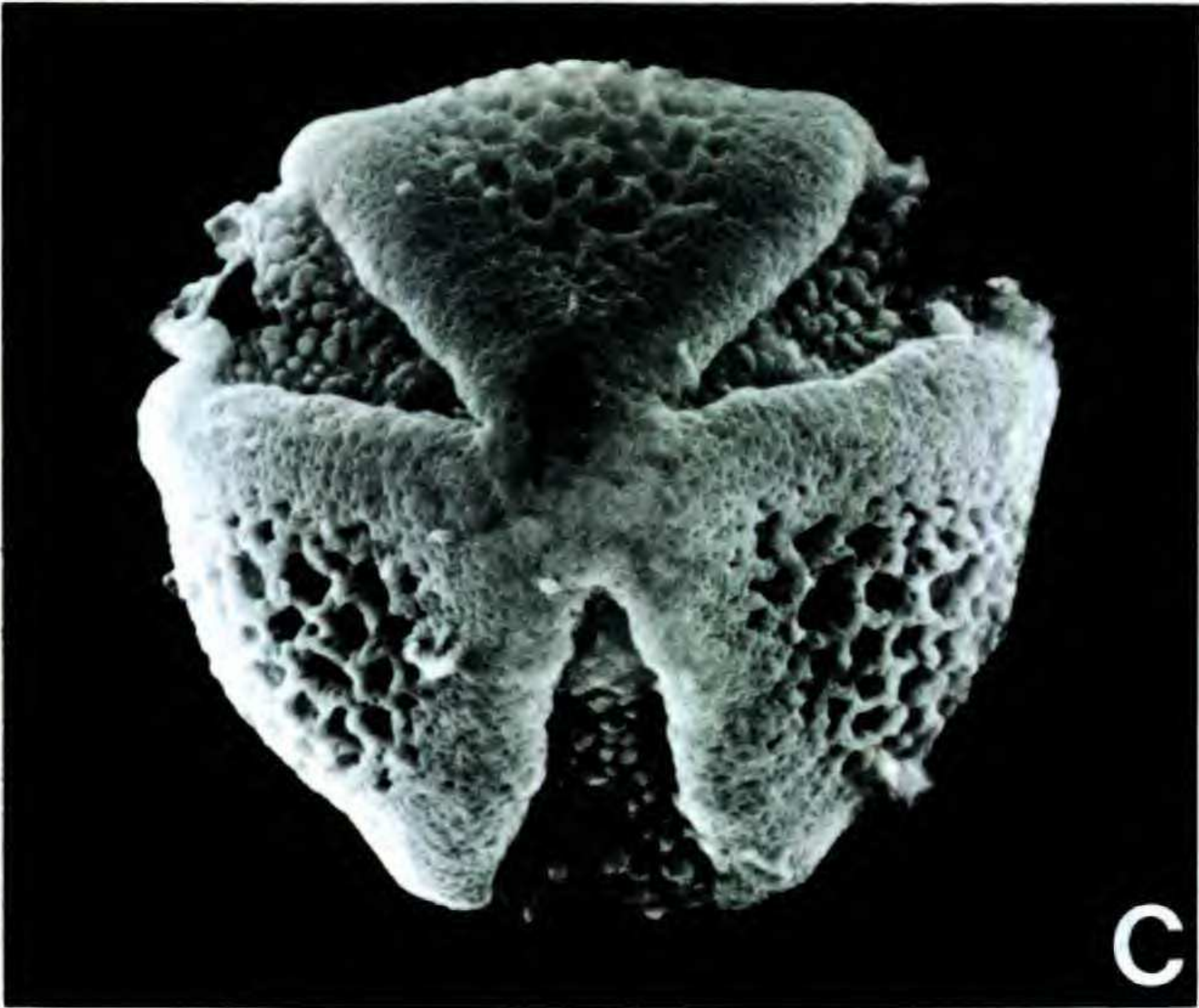
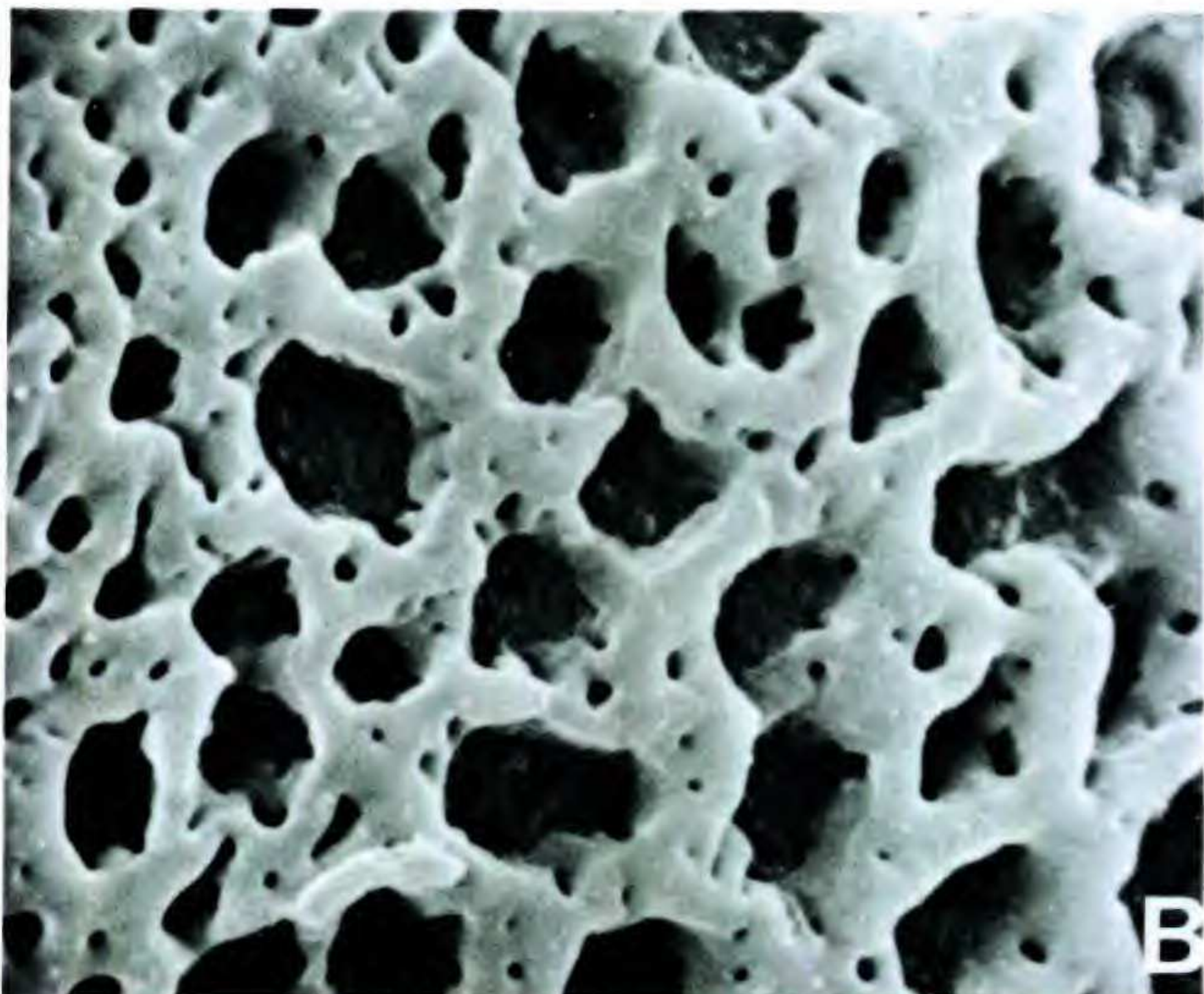
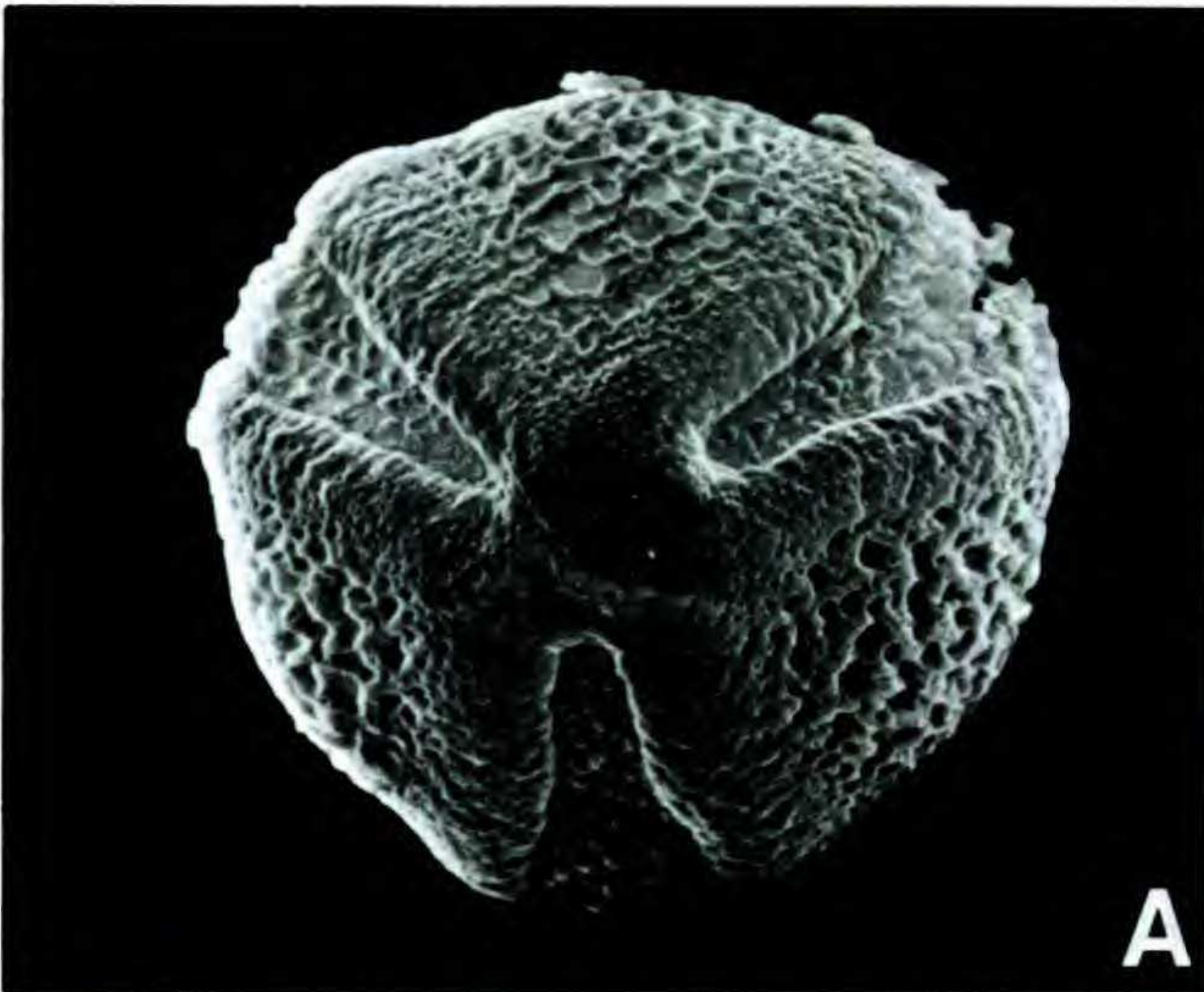
FIGURE 6.—A. *Dalbergaria cruenta*, polar view; $\times 1,516$.—B. *D. cruenta*, mesocolpial region; $\times 7,333$.—C. *D. kahlbreyeriana*, polar view; $\times 1,383$.—D. *D. kahlbreyeriana*, mesocolpial region; $\times 6,667$.—E. *D. perpulchra*, polar view; $\times 1,500$.—F. *D. perpulchra*, mesocolpial region; $\times 7,500$.—G. *D. inaequilatera*, equatorial view; $\times 1,833$.—H. *D. inaequilatera*, mesocolpial region; $\times 6,000$.

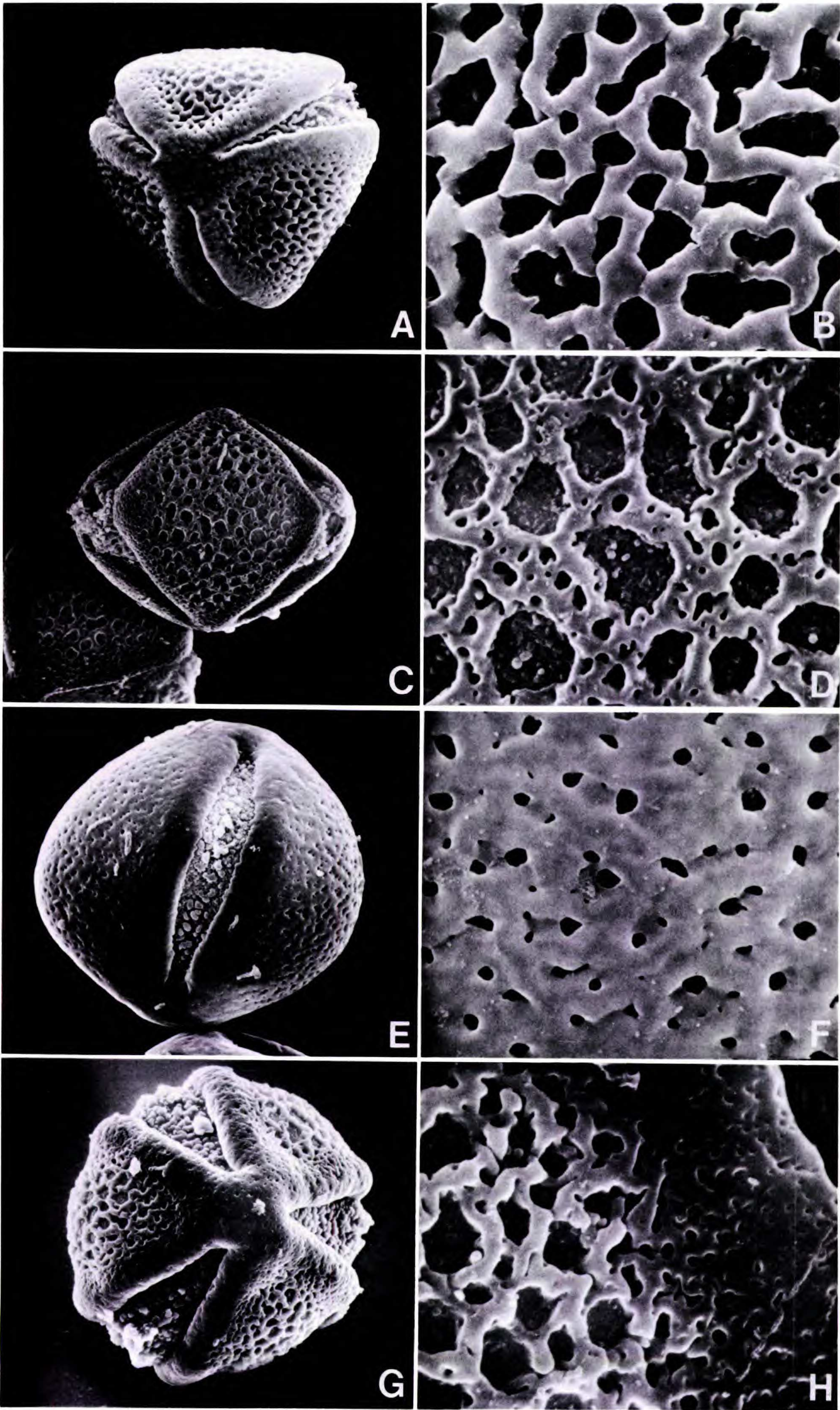
FIGURE 7.—A. *Dalbergaria vittata*, polar view; $\times 1,500$.—B. *D. vittata*, mesocolpial region; $\times 7,333$.—C. *D. ericae*, equatorial view; $\times 1,400$.—D. *D. ericae*, mesocolpial region; $\times 7,000$.—E. *D. eburnea*, equatorial view; $\times 1,500$.—F. *D. eburnea*, mesocolpial region; $\times 7,500$.—G. *D. picta*, polar view; $\times 1,367$.—H. *D. picta*, adjacent to aperture; $\times 6,833$.

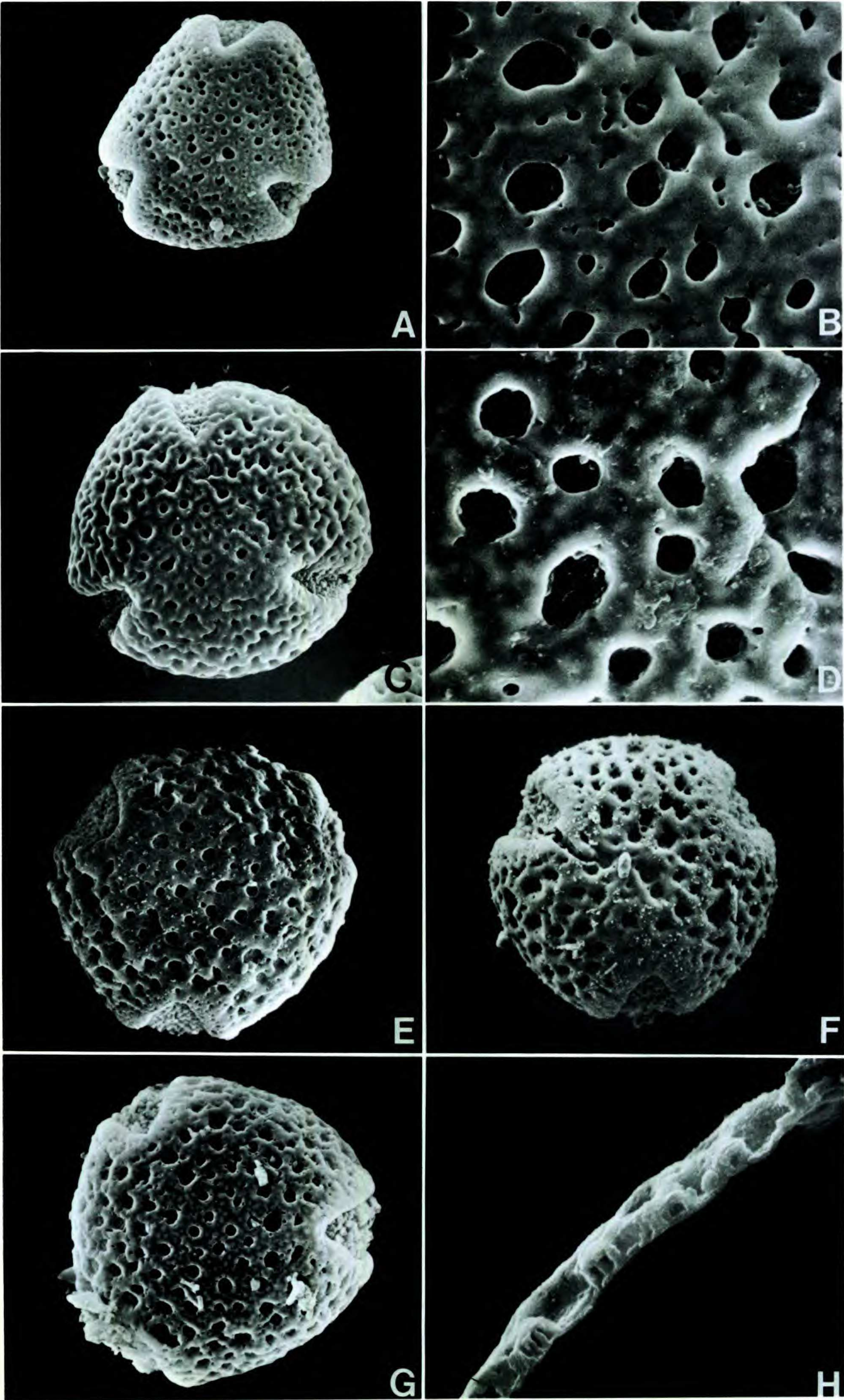
FIGURE 8.—A. *Dalbergaria florida*, polar view; $\times 1,367$.—B. *D. florida*, mesocolpial region; $\times 6,833$.—C. *D. sanguinea*, (W-1628) polar view; $\times 1,833$.—D. *D. sanguinea*, (W-1628) mesocolpial region; $\times 7,500$.—E. *D. sanguinea*, (G-85) polar view; $\times 1,517$.—F. *D. sanguinea*, (W-1709) polar view; $\times 1,443$.—G. *D. aureonitens*, polar view; $\times 1,510$.—H. *D. aureonitens*, exine fracture through mesocolpial region; $\times 5,000$.

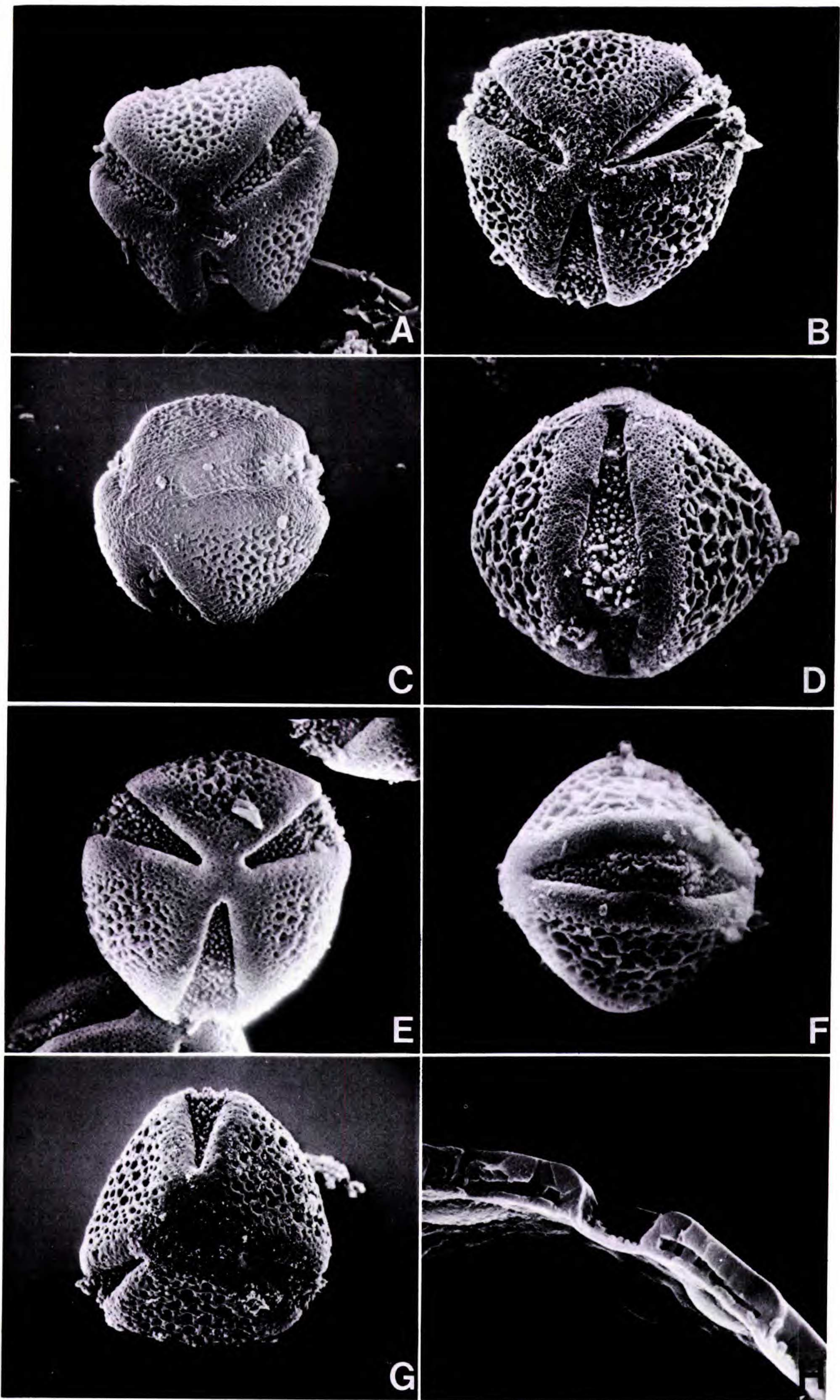
FIGURE 9.—A. *Trichantha tenensis*, polar view; $\times 1,333$.—B. *T. brenneri*, polar view; $\times 1,250$.—C. *T. pureovittata*, polar view; $\times 1,233$.—D. *T. citrina*, equatorial view; $\times 1,383$.—E. *T. mira*, polar view; $\times 1,383$.—F. *T. moorei*, equatorial view; $\times 1,283$.—G. *T. minor*, polar view; $\times 1,200$.—H. *T. calotricha*, exine fracture through mesocolpial region; $\times 4,833$.

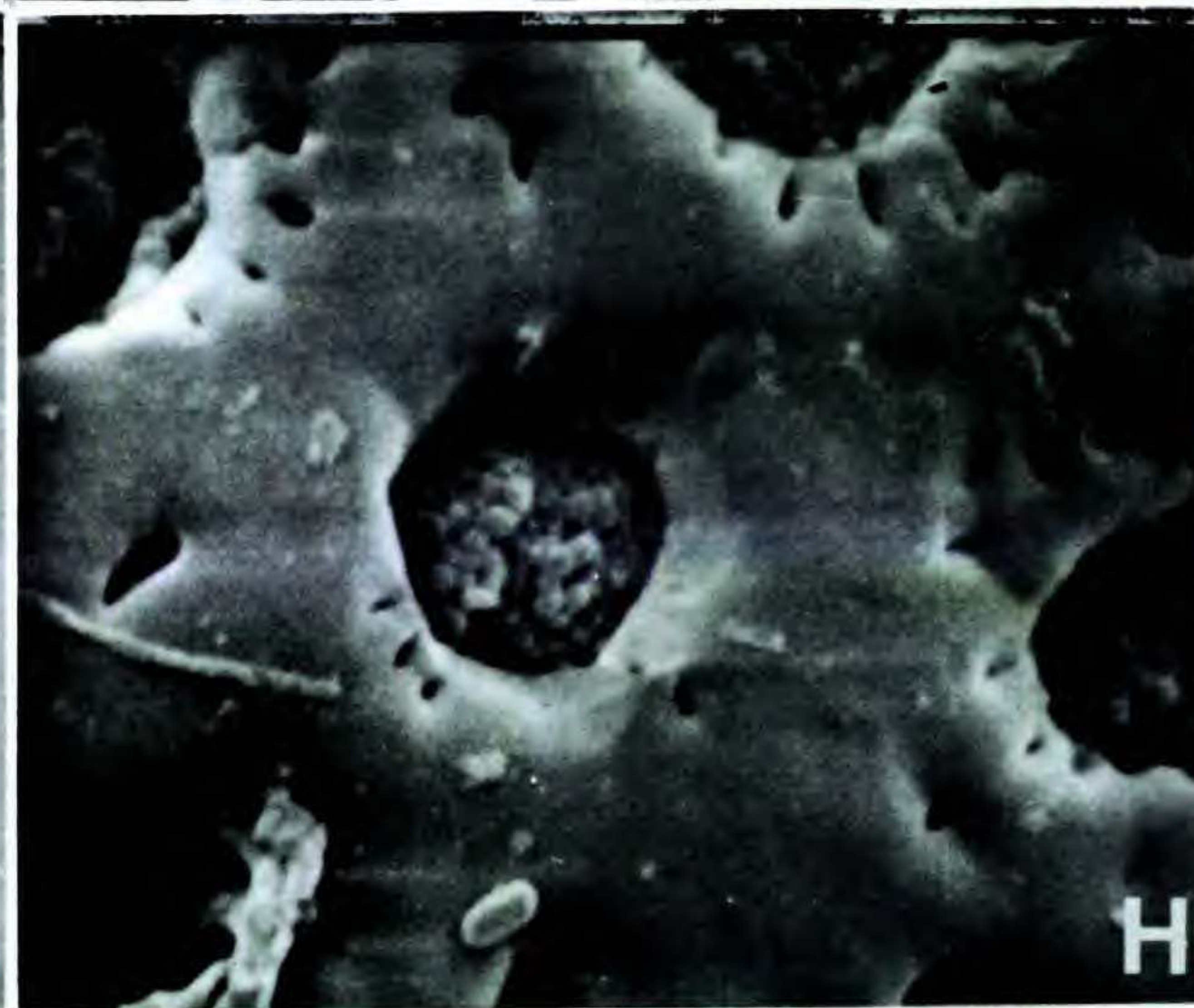
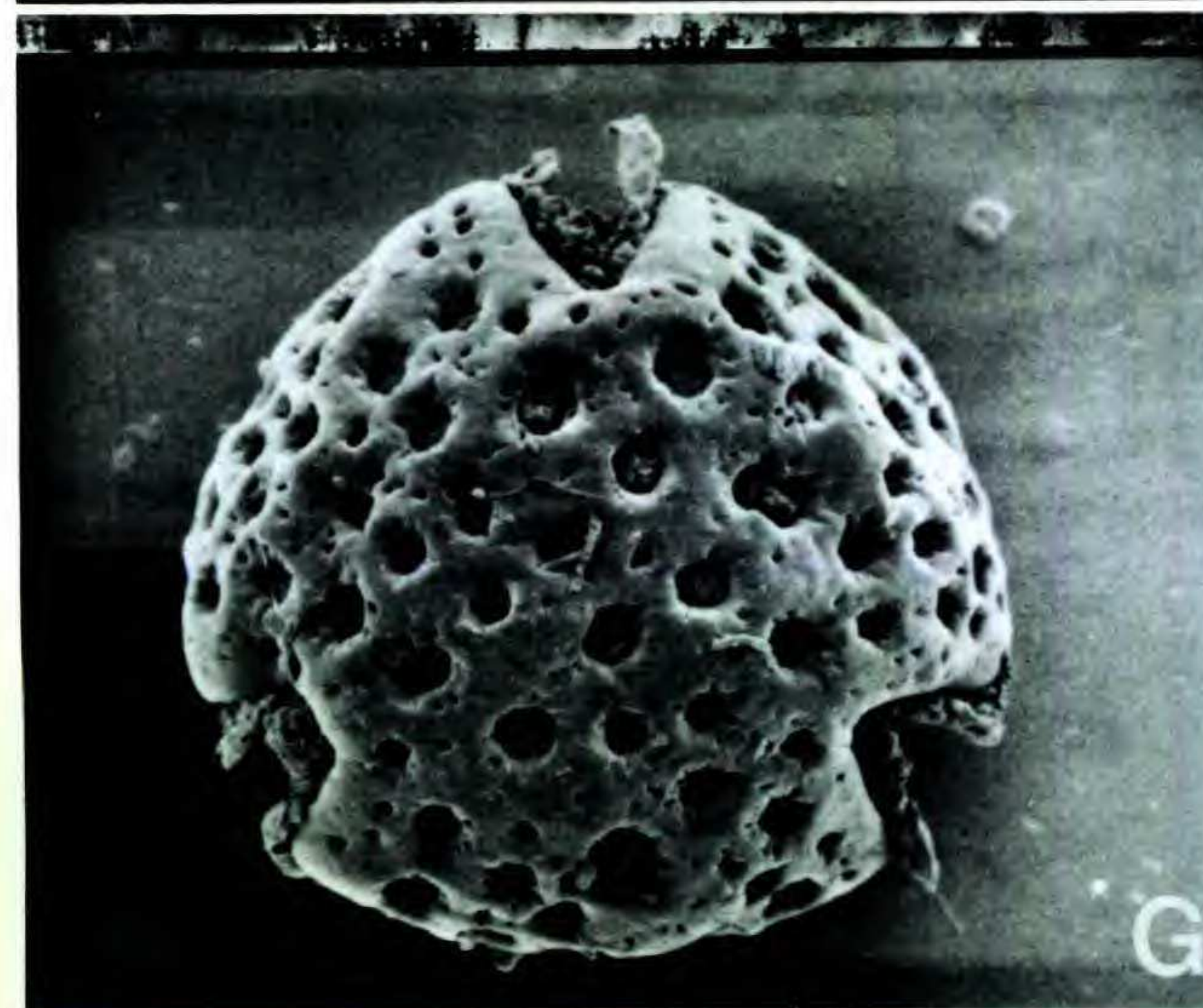
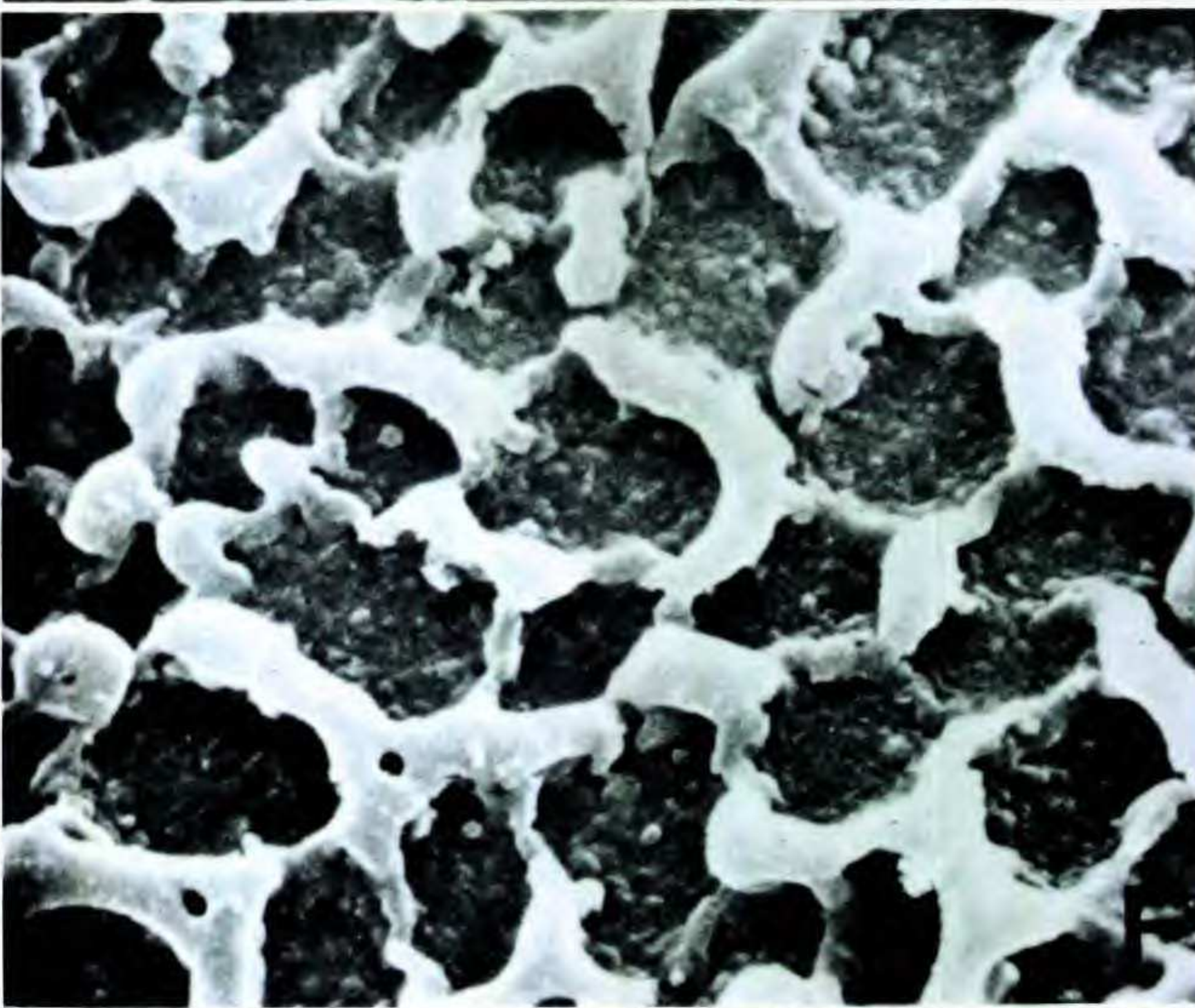
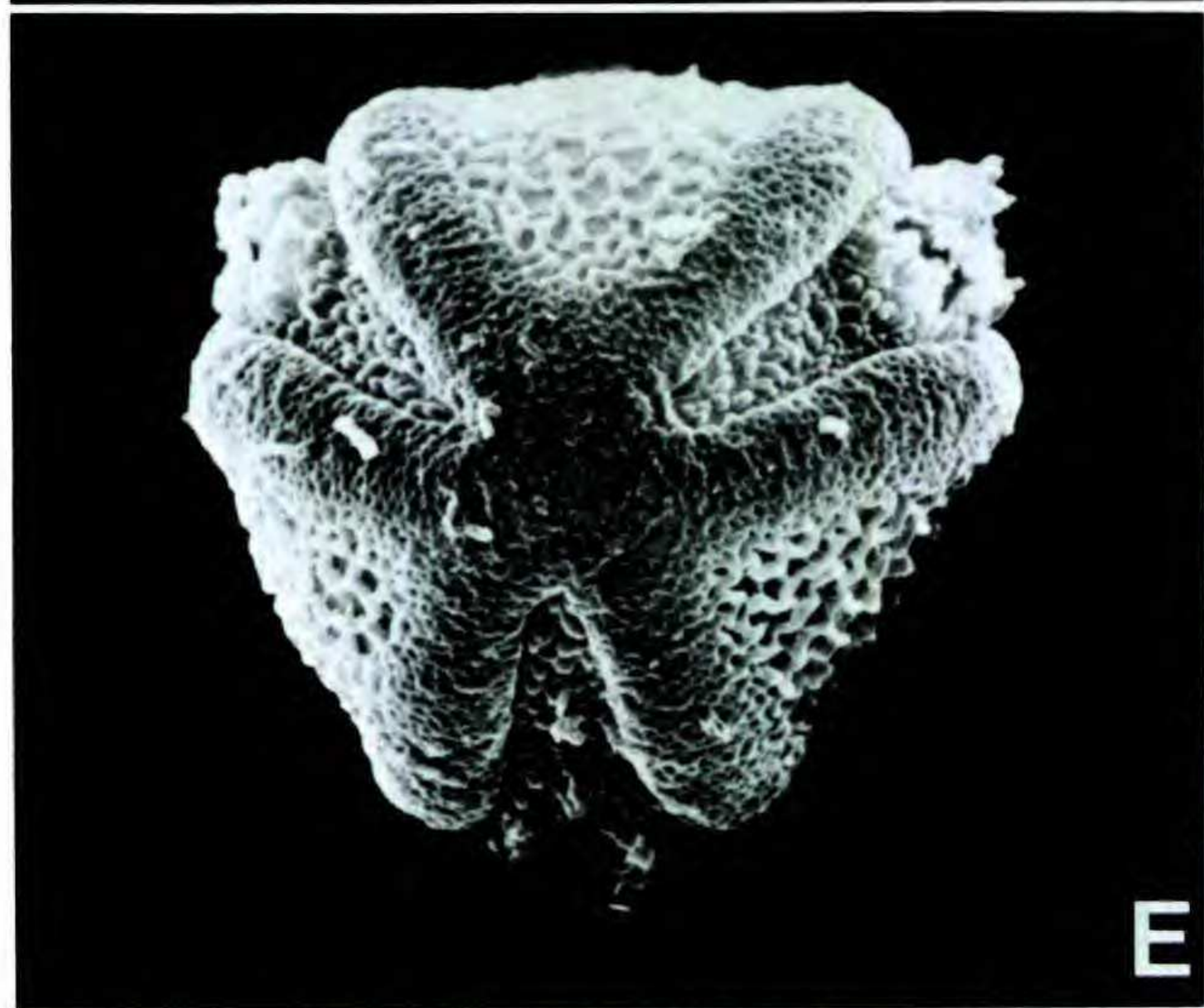
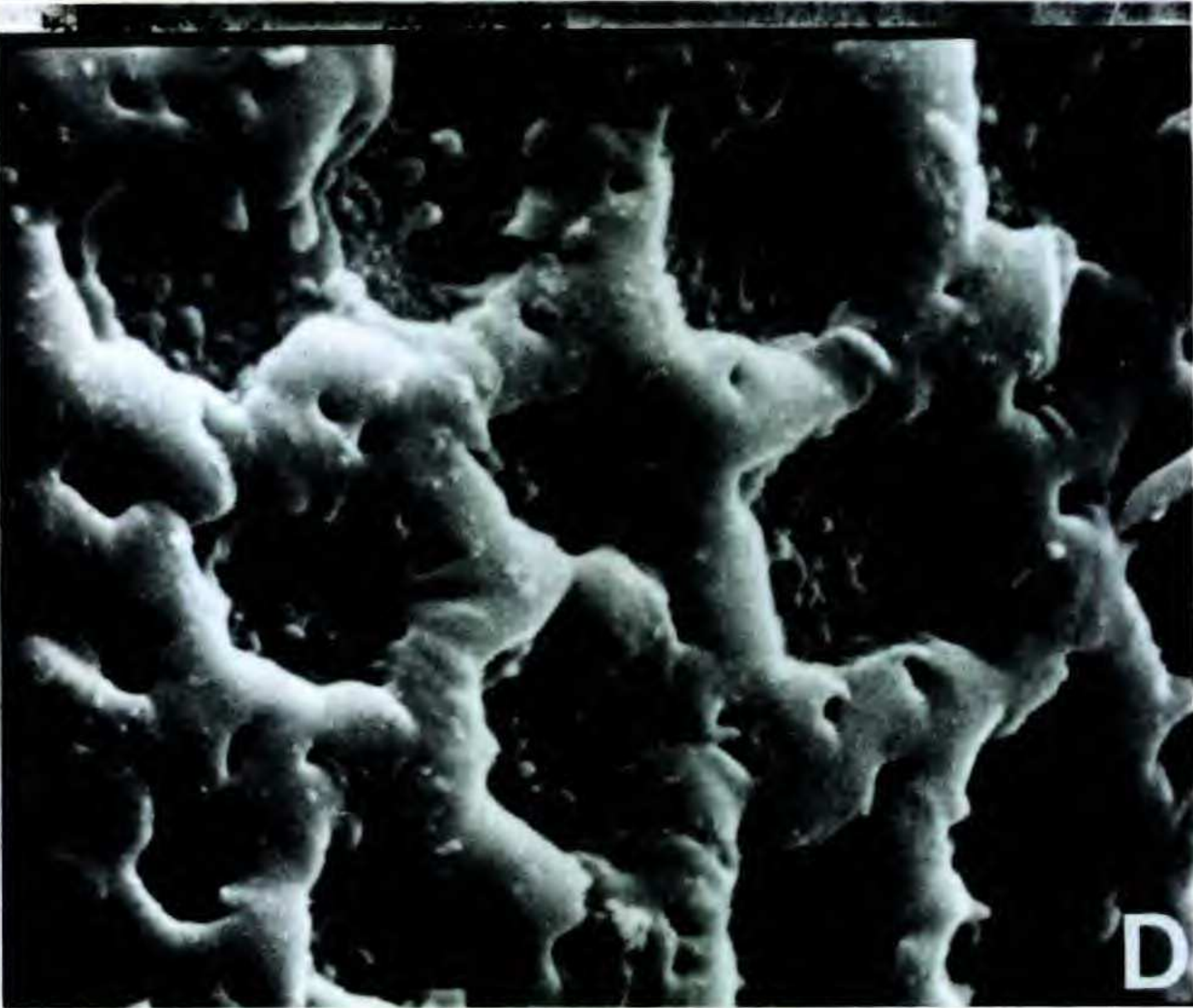
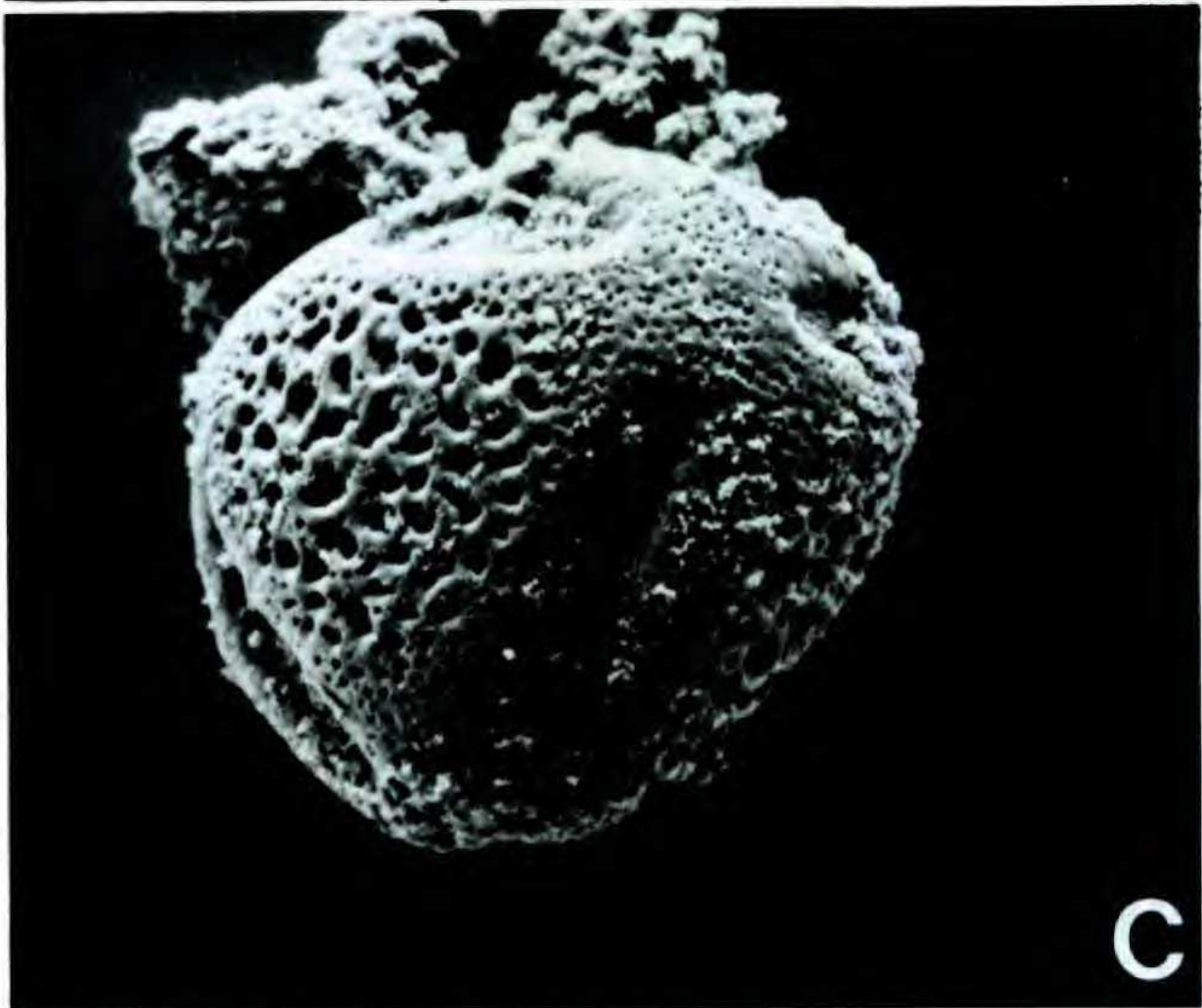
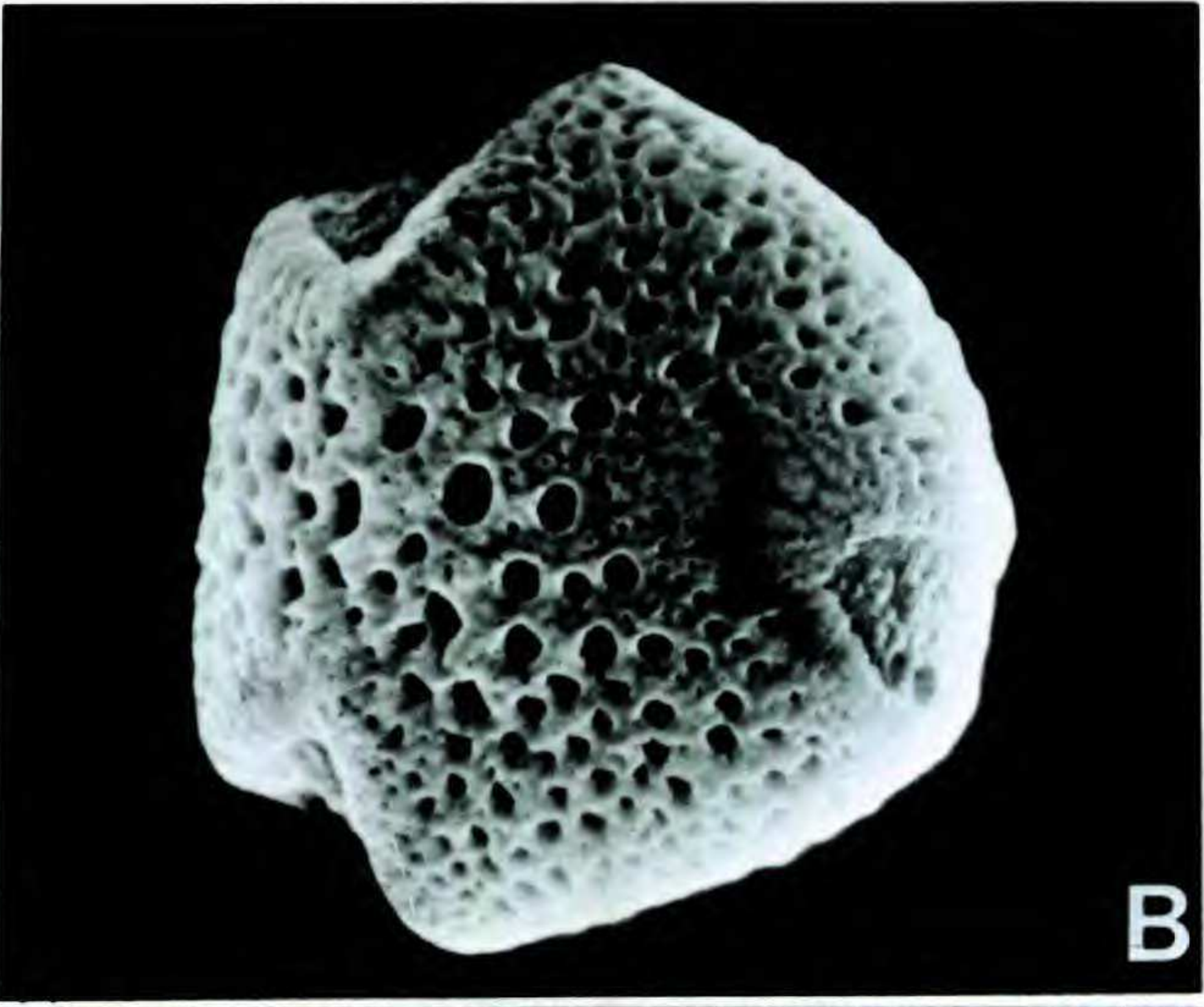
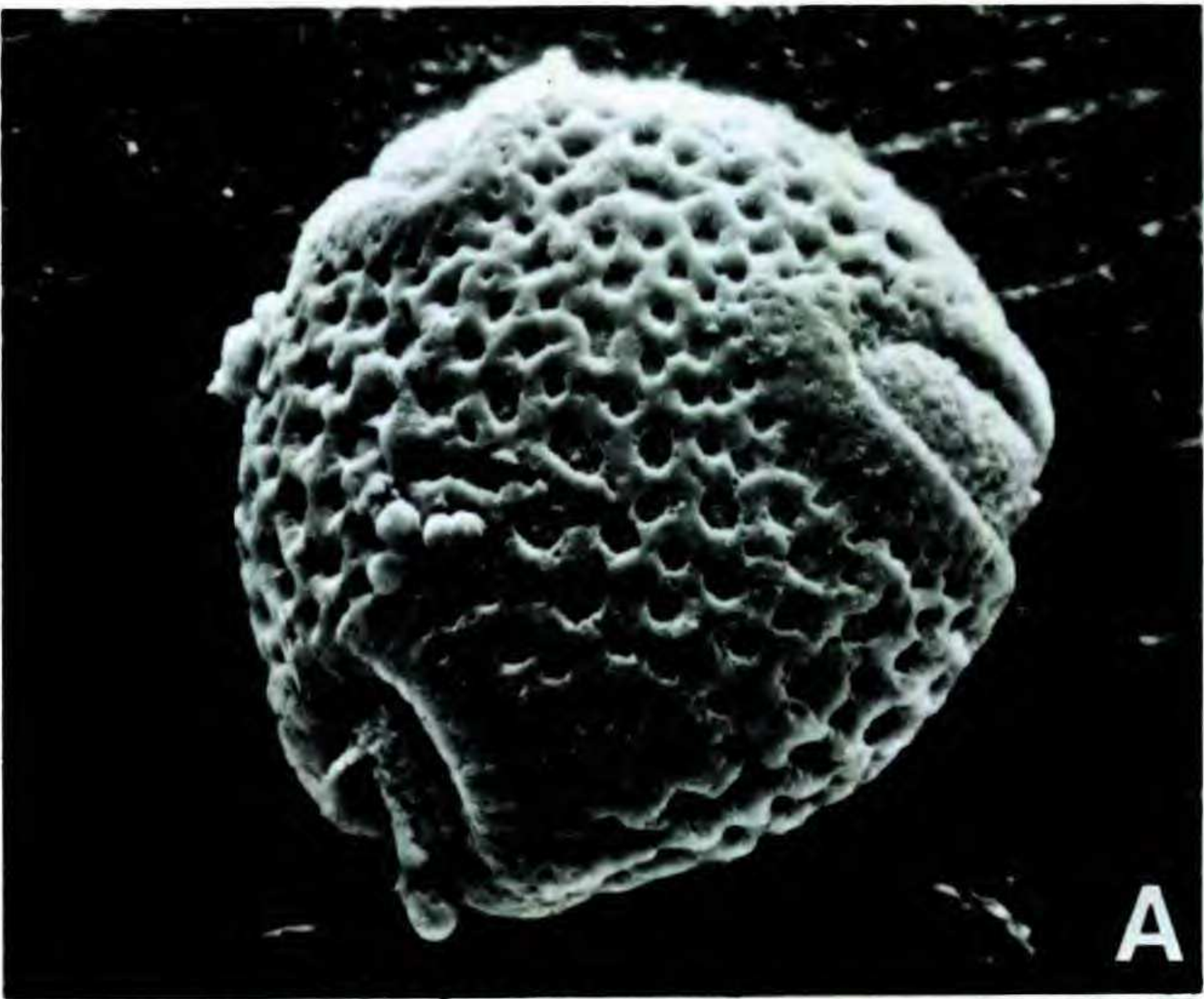
FIGURE 10.—A. *Trichantha filifera*, polar view; $\times 1,117$.—B. *T. dissimilis*, polar view; $\times 1,100$.—C. *T. ambigua*, polar/equatorial view; $\times 1,200$.—D. *T. ambigua*, mesocolpial region; $\times 6,000$.—E. *C. kucyniakii*, polar view; $\times 1,483$.—F. *C. kucyniakii*, mesocolpial region; $\times 7,333$.—G. *T. calotricha*, polar view; $\times 1,150$.—H. *T. calotricha*, mesocolpial region; $\times 6,000$.











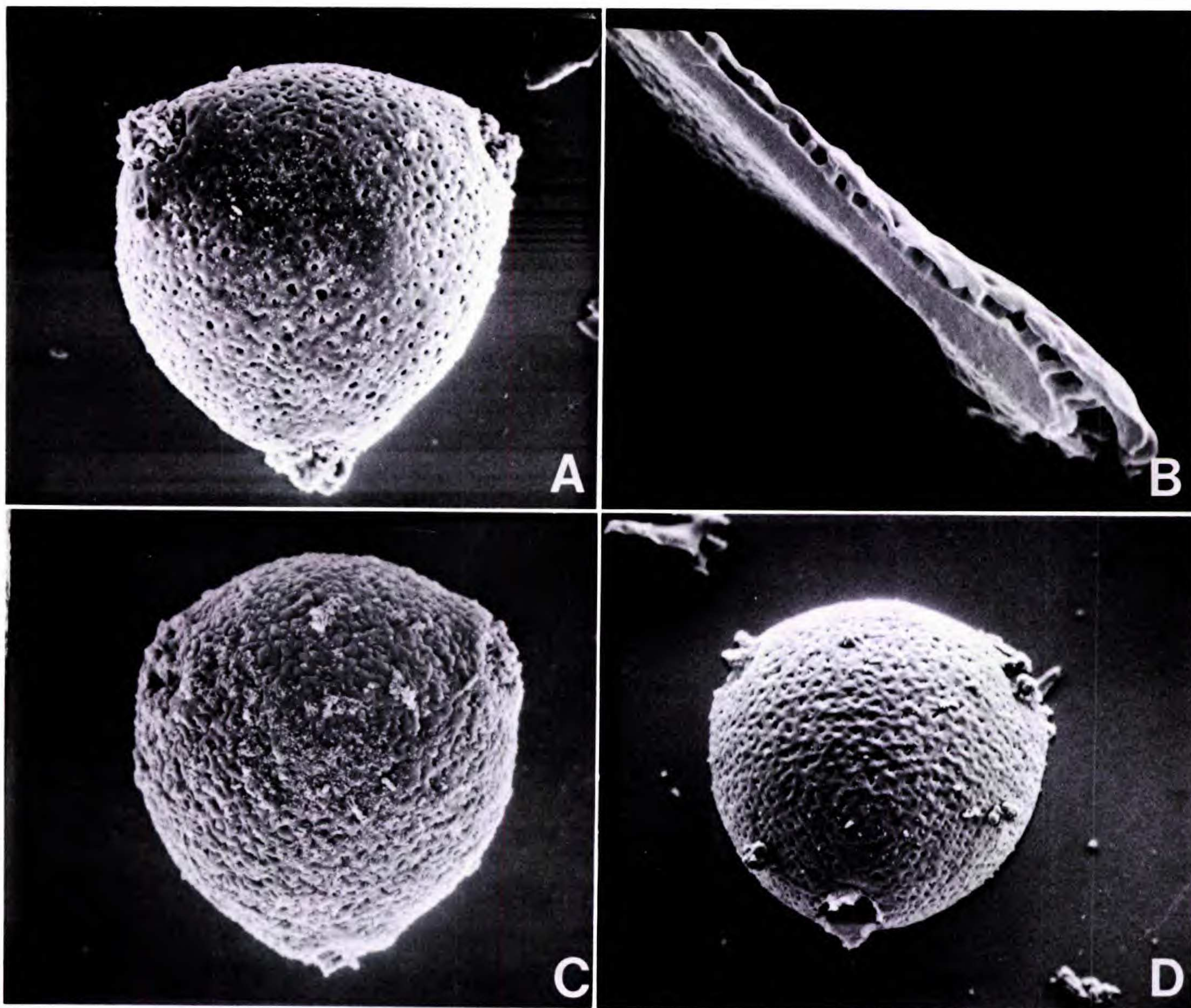


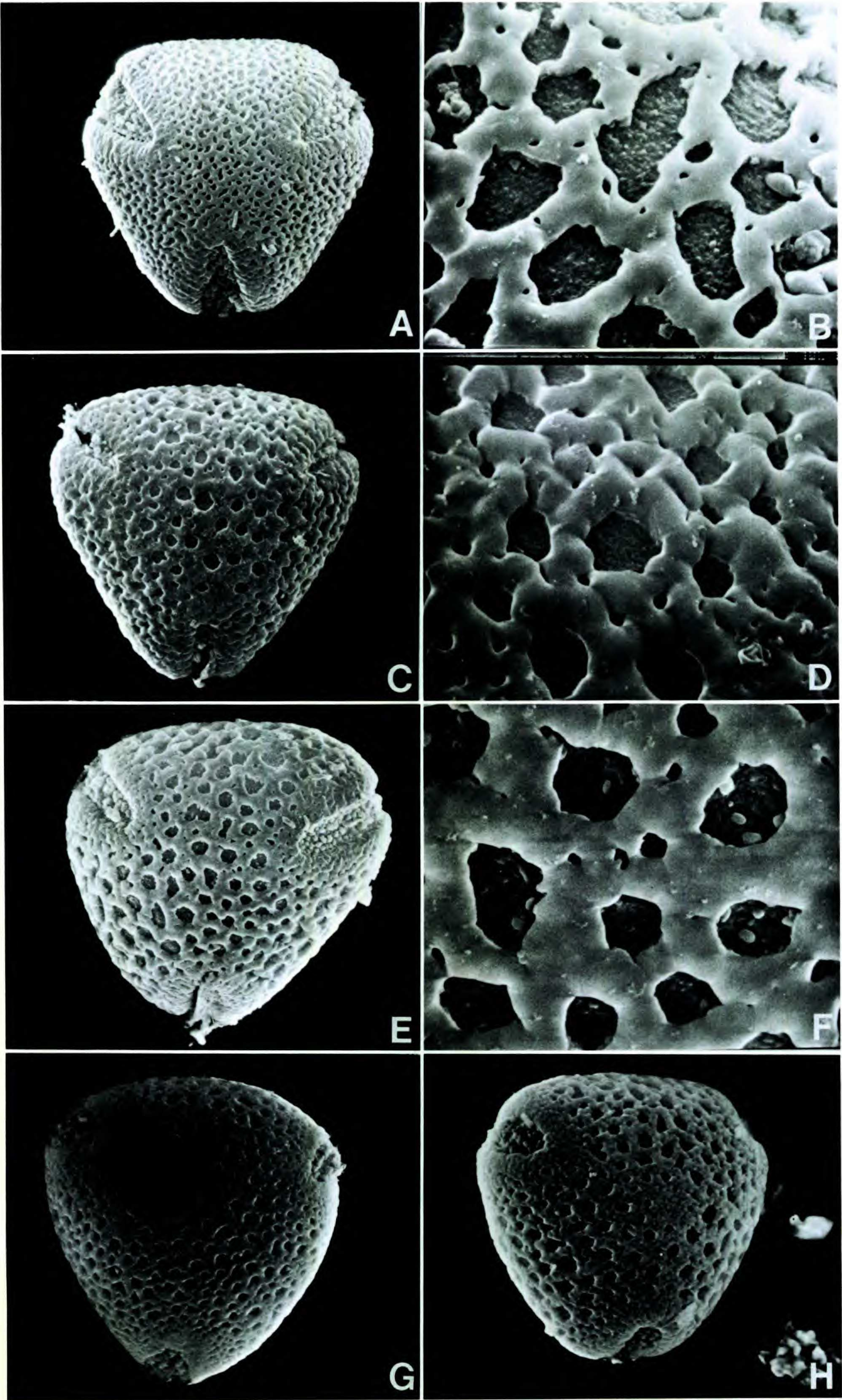
FIGURE 11.—A. *Trichantha pulchra*, polar view; $\times 1,100$.—B. *T. pulchra*, exine fracture adjacent to colpus; $\times 5,267$.—C. *T. parviflora*, polar view; $\times 1,423$.—D. *T. herthae*, polar view; $\times 1,133$.

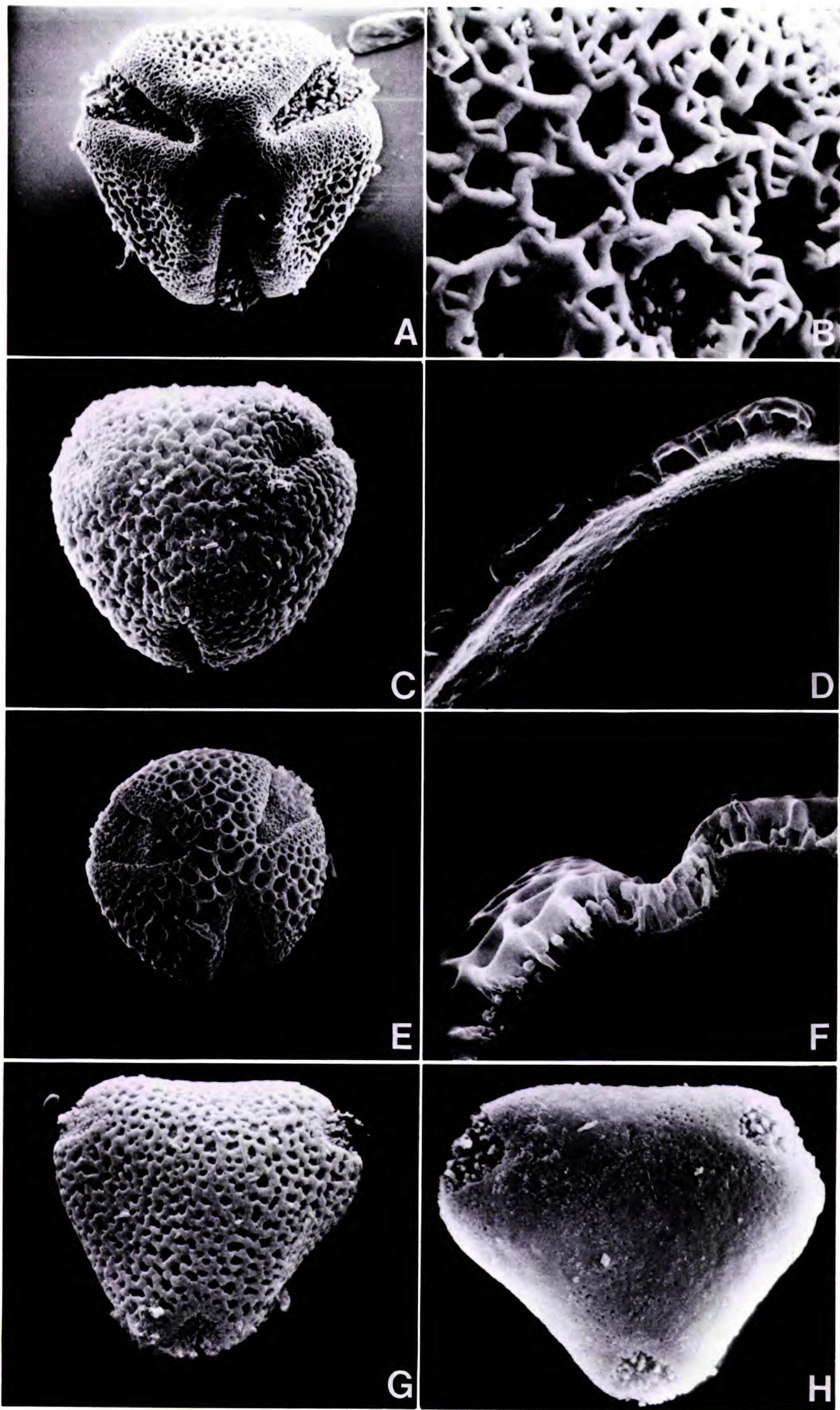
13G, H), has pollen that is readily recognizable by its extreme oblate shape, short oval apertures, and triangular ambis. The two species, however, show a sharp difference in exine patterns: *Bucinellina nariniana* has reticulate sculpturing (Fig. 13G) with wide muri, and *B. paramicola* (Fig. 13H) is nearly tectate-imperforate.

One fracture was made of each type of grain in the *Cumnea* alliance. Although they do not reveal layers visible with TEM, fractures provide useful data. One can see a di-

versity of exines, each with a different nexine-to-sexine ratio and nexine-to-tectum and columellae ratios. The exine of *Cumnea dressleri* pollen (Fig. 3H) is very uniform with closely packed columellae and a nexine-to-sexine ratio of approximately 1:6. The tectum and nexine are of equal thickness. *Dalbergaria ericae* pollen (Fig. 5H) by contrast, has a nexine-to-tectum ratio of about 1:3. The nexine-to-sexine ratio approximates 1:8. The nexine becomes thick next to the colpus, and the columellae are evenly spaced but

FIGURE 12.—A. *Pentadenia nervosa*, polar view; $\times 1,200$.—B. *P. nervosa*, mesocolpial region; $\times 7,500$.—C. *P. ecuadorana*, polar view; $\times 1,300$.—D. *P. ecuadorana*, mesocolpial region; $\times 6,000$.—E. *P. microsepala*, polar view; $\times 1,533$.—F. *P. microsepala*, mesocolpial region; $\times 7,667$.—G. *P. spathulata*, polar view; $\times 1,353$.—H. *P. zapotalana*, polar view; $\times 1,333$.





absent in the lumina. *Dalbergaria aureonitens* (Fig. 8H) has a similar exine, but the columellae are much more irregularly spaced, since they do not occur in the lumina where there is no tectum.

Trichantha calotricha pollen (Fig. 9H) has a tectum over three times thicker than the nexine. The columellae are short and vary in girth. *Trichantha pulchra* pollen (Fig. 11B) is at variance with all others examined in that its nexine is about five times thicker than the tectum and increases in thickness at the colpus. The columellae are unequally spaced and relatively short.

The nexine and tectum of *Pentadenia spathulata* (Fig. 13D) are of equal thickness, and the columellae are well spaced but absent where there is no tectum. *Pentadenia strigosa* (Fig. 13F) shows a thick tectum relative to the nexine, and baculae fill the lumina.

DISCUSSION

Pollen characters are constant, at least within certain genera and subgeneric groups, and appear to be of taxonomic use. The characters found to be most useful are overall shape, sculpturing, and aperture length. Size did not appear significant, although pollen of *Trichantha* tends to be slightly larger compared with other genera.

Some pollen forms are associated with corolla form and sometimes with general morphology of the parent plant. The more variation there is in corolla form in a genus, the more variation there is in pollen form. The cohesiveness of macromorphological characters in *Columnea* is supported by remarkable pollen uniformity; the uniformly punctate exine is characteristic of the genus. All species with this pollen type possess the characteristic galea of the flower. However, species outside the genus *Columnea* that exhibit a similar

“columnneoid” corolla do not have the pollen characteristics of *Columnea* (*Dalbergaria picta*, *D. ericae*, *D. kalbreyeriana*).

Pollen of *Columnea repens* and *C. rutilans*, the only two columnneas examined that occur outside the mainland of Central and South America, is different from that of mainland species (Figs. 5B, C). These two species are endemic to Jamaica, and different selection pressures there could be a factor in their divergence from the general pattern. *Columnea kucyniakii* does not fit very well with the remainder of the genus *Columnea*. Its pollen is more similar to the pollen of *Dalbergaria* or *Trichantha*, but the species does not easily fit into the concept of either of the genera in terms of floral features and general habit (Wiehler, pers. comm.).

The two species of *Bucinellina* share the same grain shape and aperture size, but they have different exine patterns and a slight difference in grain size. They are from the same general locality, and their flowers and habit are fairly similar; the reason for the pollen difference is not evident.

Trichantha purpureovittata, *T. tenensis*, and *T. brenneri* are closely related and have similar corollas as well as similar general plant habit (Wiehler, 1975). The similarity of their pollen correlates well with these characters. *Trichantha pulchra*, *T. herthae*, and *T. parviflora* make up another group of morphologically similar species (Wiehler, 1977, pers. comm.). They have small yellow corollas with tough, incurved lobes and similar pollen. *Trichantha calotricha* has a corolla similar to those of the rest of this group, but its pollen is very different. *Trichantha citrina* and *T. mira* are also closely related to each other (Wiehler, 1978), and their pollen reflects this relationship.

Dalbergaria species have similar pollen and a moderate degree of uniformity in their

←

FIGURE 13. —A. *Pentadenia orientandina*, polar view; $\times 1,400$. —B. *P. orientandina*, mesocolpial region; $\times 7,333$. —C. *P. angustata*, polar view; $\times 1,467$. —D. *P. spathulata*, exine fracture near colpus (far right); $\times 7,083$. —E. *P. strigosa* polar view; $\times 1,467$. —F. *P. strigosa*, exine fracture at polar end of colpus; $\times 5,067$. —G. *Bucinellina nariniana*, polar view; $\times 1,467$. —H. *B. paramicola*, polar view; $\times 1,633$.

TABLE 2. Summary of pollen characters in the *Columnnea* alliance. *p* = punctate, *r* = reticulate, *s* = short, *l* = long, *i* = intermediate, *c* = circular, *a* = angular, *e* = elliptic, *o* = oval, *n* = narrow, *t* = tapered at poles; *P/E* = ratio of polar axis length to equatorial axis length.

Species	P/E	Sculpture			Colpus		
		Apocol- pium	Mesocol- pium	Colpus Border	Length	Shape	Amb
<i>Columnnea arguta</i>	1.20	p	p	p	l	e	c
<i>C. bilabiata</i>	—	p	p	p	l	et	c
<i>C. billbergiana</i>	—	p	p	p	l	e	c
<i>C. cobana</i>	0.92	p	p	p	l	et	c
<i>C. dodsonii</i>	—	p	p	p	l	e	c
<i>C. dressleri</i>	1.12	p	p	p	l	e	c
<i>C. erythrophaea</i>	—	p	p	p	l	e	c
<i>C. flaccida</i>	—	p	p	p	l	e	c
<i>C. gallicauda</i>	—	p	p	p	l	e	c
<i>C. gloriosa</i>	—	p	p	p	l	e	c
<i>C. guatemalensis</i>	1.10	p	p	p	l	e	c
<i>C. hirsutissima</i>	1.04	p	p	p	l	e	c
<i>C. kienastiana</i>	1.02	p	p	p	l	et	c
<i>C. kucyniakii</i>	—	p	r	p	l	t	a
<i>C. linearis</i>	1.09	p	p	p	l	e	c
<i>C. maculata</i>	1.16	p	p	p	l	e	c
<i>C. nicaraguensis</i>	—	p	p	p	l	e	c
<i>C. oerstediana</i>	—	p	p	p	l	e	c
<i>C. purpusii</i>	0.99	p	p	p	l	e	c
<i>C. querceti</i>	0.99	p	p	p	l	e	c
<i>C. repens</i>	0.72	p	r	p	l	t	a
<i>C. rubra</i>	—	p	p	p	l	e	c
<i>C. rubricaulis</i>	—	p	p	p	l	e	c
<i>C. rutilans</i>	0.89	p	r	p	l	t	a
<i>C. schiedeana</i>	0.94	p	p	p	l	e	c
<i>C. verecunda</i>	0.90	p	p	p	l	e	c
<i>C. zebranella</i>	1.10	p	p	p	l	et	c
<i>Dalbergaria asteroloma</i>	—	p	r	p	l	n	c
<i>D. aureonitens</i>	0.89	r	r	p	i	e	c
<i>D. cruenta</i>	0.78	p	r	p	l	t	a
<i>D. eburnea</i>	0.89	p	p	p	l	nt	a
<i>D. ericae</i>	0.76	p	r	p	l	t	a
<i>D. florida</i>	0.84	r	r	p	i	e	a
<i>D. inaequilatera</i>	0.78	p	r	p	l	t	a
<i>D. kahlbreyeriana</i>	—	p	r	p	l	t	a
<i>D. perpulchra</i>	0.78	p	r	p	l	t	a
<i>D. picta</i>	0.85	p	r	p	l	t	a
<i>D. polyantha</i>	0.76	p	r	p	l	t	c
<i>D. puyana</i>	0.86	p	r	p	l	t	a
<i>D. sanguinea</i> ¹	—	r	r	p	i	e	c
<i>D. sanguinea</i> ²	—	r	r	p	i	e	c
<i>D. sanguinea</i> ³	0.91	r	r	p	i	et	c
<i>D. silvarum</i>	0.70	p	r	p	l	t	c
<i>D. vittata</i>	0.80	p	r	p	l	t	a
<i>Pentadenia angustata</i>	—	r	r	p	i	n	a
<i>P. byrsina</i>	—	r	r	p	i	t	a
<i>P. ecuadorana</i>	0.75	r	r	p	i	n	a
<i>P. microsepala</i>	—	r	r	p	i	n	a
<i>P. nervosa</i>	—	r	r	p	i	t	a
<i>P. orientandina</i>	—	p	r	p	l	t	a

TABLE 2. Continued.

Species	P/E	Sculpture			Colpus		
		Apocol- pium	Mesocol- pium	Colpus Border	Length	Shape	Amb
<i>P. spathulata</i>	—	r	r	p	s	e	a
<i>P. strigosa</i>	0.82	r	r	r	l	t	c
<i>P. zapotalana</i>	—	p	r	p	s	e	a
<i>Trichantha ambigua</i>	—	p	r	p	i	n	a
<i>T. brenneri</i>	—	p	r	p	l	t	a
<i>T. calotricha</i>	0.79	r	r	p	i	e	a
<i>T. citrina</i>	0.80	p	r	p	l	t	a
<i>T. dissimilis</i>	0.66	r	r	p	i	e	a
<i>T. filifera</i>	—	r	r	p	i	e	a
<i>T. herthae</i>	0.86	p	p	p	s	o	c
<i>T. minor</i>	0.86	p	r	p	l	t	a
<i>T. mira</i>	0.75	p	r	p	l	t	c
<i>T. moorei</i>	0.85	p	r	p	l	t	a
<i>T. parviflora</i>	—	p	p	p	s	o	c
<i>T. pulchra</i>	—	p	p	p	s	o	c
<i>T. purpureovittata</i>	0.94	p	r	p	l	t	a
<i>T. tenensis</i>	0.79	p	r	p	l	t	a
<i>Bucinellina paramicola</i>	—	p	p	p	s	o	a
<i>B. nariniana</i>	—	r	r	p	s	o	a

¹ Accession number W-1709.
² Accession number G-85.
³ Accession number W-1628.

corollas. Most pollen grains show slight variations on a theme, e.g., long apertures and a tectum punctate around the colpi and at the poles. Pollen of *Dalbergaria sanguinea*, a tetraploid, is no larger than that of the rest of the genus but is distinct by showing no reduction of the reticulum at the poles and by having apertures of intermediate length. *Dalbergaria aureonitens* is closely related to *D. sanguinea* (Wiehler, 1973), which is reflected by pollen similarities between them. *Dalbergaria florida* is somewhat atypical in the genus although its pollen exhibits features that closely resemble *Dalbergaria sanguinea* and *D. aureonitens*.

In *Pentadenia* there is a relatively high degree of uniformity in corolla forms (Wiehler, pers. comm.) and in the pollen. Most corollas are tubular, small, and generally nondescript. *Pentadenia strigosa*, however, is strikingly different from the rest of the species in the alliance in its much larger corolla and peculiar pollen characteristics, probable adaptations to pollination by bats.

The Gesneriaceae are placed in the relatively advanced order Scrophulariales, and the reticulate, tricolpate pollen of Gesneriaceae is advanced among dicotyledons (Walker & Doyle, 1975). This family has a specialized shape in that it departs from the spherical. The exine pattern is specialized as it differs from the primitive tectate grain. A reduction in aperture size can be seen, particularly in the Episcieae.

Some similarities to pollen of other families in the order Scrophulariales can be seen in pollen of the Gesneriaceae. In the Scrophulariaceae and Myoporaceae one finds tricolpate pollen (Niezgoda & Tomb, 1975) and finely reticulate exines reminiscent of *Columnea*. The colpi are long, but the apertures are diorate, a rare type not found in the Gesneriaceae. Erdtman (1966) found tri-colp(or)ate, oblate-spheroidal, subprolate, or prolate-spheroidal pollen in the Scrophulariaceae. These attributes are within the range of pollen features of the Gesneriaceae.

Boj (1961) made an extensive survey of

the Acanthaceae and found few features that can be compared to the Gesneriaceae other than the reticulate exine. Erdtman (1966) examined 55 species in 35 genera of Acanthaceae and found it to have uniform pollen. One tricolporoid type is subprolate to prolate and has fine reticulation in which the brochi decrease in size toward the colpi. The grains are also within the size range found in the Gesneriaceae.

Buurman (1977) found a number of features in Bignoniaceae similar to those of gesneriaceous pollen. The number of apertures varies, but the tricolpate type exhibits a prolate shape and a uniformly punctate tectum, the lumina of which decrease (almost imperceptibly) in size adjacent to the colpi. These features are predominant in Gesneriaceae tribe Gloxineae (see Williams, 1978). Buurman (1977) outlined within the tricolpate group some evolutionary trends that may have some application to the Gesneriaceae (see below). Erdtman (1966) examined pollen of 25 species in 20 bignoniaceous genera and found a size range that exceeds that of the Gesneriaceae.

This study has answered several questions regarding pollen use in taxonomic considerations of the *Columnea* alliance. Pollen characters separate *Columnea* and *Bucinellina* from the rest of the alliance, but there is much variation within the other genera. Pollen appears to be useful, however, in several ways. Subgeneric groups that exhibit similar pollen could be classified as sections, since they are found to be closely related by other criteria. Differences between species in some pollen features are more apparent than differences between genera, so pollen characters seem to be good species indicators. Pollen does appear to be useful for separating the *Columnea* alliance from other alliances and other alliances from each other.

Evolutionary trends based on the pollen information gathered here can be related to Buurman's (1977) scheme. Tectal features in the *Columnea* alliance exhibit a trend from perforate to uniformly reticulate to punctate near colpi and at poles. Caution must be exercised when this scheme is applied to the

Columnea alliance, however, since next to *Bucinellina*, *Columnea* is considered most advanced, but it has a uniformly punctate tectum. The shape and size of the grains in the *Columnea* alliance exhibit a trend from spherical and small to oblate or prolate and large. We postulate that the ancestral pollen was tricolpate, spherical, and uniformly reticulate with small lumina, much like pollen that occurs in the tribe Gloxineae (Williams, 1978).

LITERATURE CITED

- BOJ, R. 1961. Pollen morphological studies in the Acanthaceae. *Grana Palynol.* 3: 3-108.
- BURT, B. L. 1963. Studies in the Gesneriaceae of the Old World. XXIV: tentative keys to the tribes and genera. *Notes Roy. Bot. Gard. Edinburgh* 24: 205-220.
- BUURMAN, J. 1977. Contributions to the pollen morphology of the Bignoniaceae with special reference to the tricolpate type. *Pollen & Spores* 19: 447-519.
- ERDTMAN, G. 1966. *Pollen Morphology and Plant Taxonomy*. Hafner Publishing Co., New York.
- FRITZE, K. 1979. *Pollen Morphology and the Taxonomy of the Columnea Alliance (Gesneriaceae: Gesnerioideae)*. M.S. Thesis. Florida State University, Tallahassee, Florida.
- MELHEM, T. S. & C. MAURO. 1973. Pollen morphological studies in Gesneriaceae. *Hoehnea* 3: 13-27.
- MOORE, H. E. & R. E. LEE. 1967. The broadening basis of classification in the Gesneriaceae. *Baileya* 15: 97-108.
- MORLEY, B. D. 1971. A hybrid swarm between two hummingbird-pollinated species of *Columnea* (Gesneriaceae) in Jamaica. *Bot. J. Linn. Soc.* 64: 81-96.
- . 1972a. The distribution and variation of some gesneriads on Caribbean islands. Pp. 239-257 in D. H. Valentine (editor), *Taxonomy, Phytogeography, and Evolution*. Academic Press, New York.
- . 1972b. Some karyotype diversity in *Columnea* L. *sensu lato* (Gesneriaceae). *Bot. J. Linn. Soc.* 65: 25-36.
- . 1973. Ecological factors of importance to *Columnea* taxonomy. Pp. 265-281 in V. H. Heywood (editor), *Taxonomy and Ecology*. Academic Press, New York.
- . 1974. Notes on some critical characters in *Columnea* classification. *Ann. Missouri Bot. Gard.* 61: 514-525.
- . 1976. A key, typification and synonymy of the sections in the genus *Columnea* L. (Gesneriaceae). *Contr. Natl. Bot. Gard. Glasnevin* 1: 1-11.
- MORTON, C. V. 1963. A revision of *Trichantha* (Gesneriaceae). *Contr. U.S. Natl. Herb.* 38: 1-27.
- . 1971. A reduction of *Trichantha* to *Columnea* (Gesneriaceae). *Phytologia* 22: 223-224.
- NIEZGODA, C. T. & A. S. TOMB. 1975. Systematic

- palynology of the tribe Leucophylleae (Scrophulariaceae) and selected Myoporaceae. *Pollen & Spores* 17: 495-516.
- SHERK, L. C. & R. E. LEE. 1967. Interspecific hybridization in the genus *Columnea* (Gesneriaceae). *Baileya* 15: 89-96.
- SKOG, L. E. 1976. A study of the tribe Gesnerieae, with a revision of *Gesneria* (Gesneriaceae: Gesnerioideae). *Smithsonian Contr. Bot.* 29: 1-182.
- WALKER, J. W. 1974a. Evolution of exine structure in the pollen of primitive angiosperms. *Amer. J. Bot.* 61: 891-902.
- . 1974b. Aperture evolution in the pollen of primitive angiosperms. *Amer. J. Bot.* 61: 1112-1136.
- & J. A. DOYLE. 1975. The bases of angiosperm phylogeny: palynology. *Ann. Missouri Bot. Gard.* 62: 664-723.
- & E. S. KEMP. 1972. Preliminary studies of exine stratification in the pollen of primitive angiosperms. *Brittonia* 24: 129-130. [Abstract.]
- WIEHLER, H. 1971. Name changes for some American Gesneriaceae in cultivation. *Baileya* 18: 133-138.
- . 1973. One hundred transfers from *Alloplectus* and *Columnea* (Gesneriaceae). *Phytologia* 27: 309-329.
- . 1975. Three new species of *Trichantha* from Ecuador and Peru (Gesneriaceae). *Selbyana* 1: 36-43.
- . 1977. New genera and species of Gesneriaceae from the Neotropics. *Selbyana* 2: 67-132.
- . 1978. Miscellaneous transfers and new species of neotropical Gesneriaceae. *Selbyana* 5: 61-93.
- . 1983. A synopsis of the neotropical Gesneriaceae. *Selbyana* 6: 1-219.
- WILLIAMS, N. H. 1978. Pollen structure and the systematics of the neotropical Gesneriaceae. *Selbyana* 2: 310-322.
- WILSON, C. L. 1974. Floral anatomy in Gesneriaceae. II. Gesnerioideae. *Bot. Gaz. (Crawfordsville)* 135: 256-268.
- WOODS, P. 1964. Pollen morphology in Gesneriaceae. 10th International Botanical Congress, Edinburgh, p. 97. [Abstract.]